

A REVISION OF THE GENUS
GENTIANELLA
IN NEW ZEALAND

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Abstract

Previous work on *Gentianella* and related genera is reviewed, particularly the taxonomic history of the New Zealand gentians and their generic placement. Phylogenetic analysis of DNA sequences show the New Zealand gentians belong in *Gentianella*.

Thirty species are recognised, including seven species (*G. angustifolia*, *G. calcis*, *G. decumbens*, *G. luteoalba*, *G. impressinervia*, *G. scopulorum*, and *G. stellata*) described as new, and one (*G. magnifica*) raised from varietal status. The identity of *G. patula* is clarified. The specific status of *G. amabilis* is affirmed. Thirteen subspecies are recognised, including a new subspecies within *G. astonii* (subsp. *arduana*) and four within a new species *G. calcis* (subsp. *calcis*, subsp. *waipara*, subsp. *manahune*, subsp. *taiko*). New subspecies are also made in *G. corymbifera* (subsp. *gracilis*), *G. montana* (subsp. *ionostigma*), and *G. chathamica* (subsp. *nemorosa*). *G. montana* var. *stolonifera* Cheeseman is the only existing variety that this treatment continues to recognise. Four species recognised by Allan (1961) are reduced to synonymy (*G. gracilifolia*, *G. matthewsii*, *G. tereticaulis*, and *G. townsonii*). Descriptions and keys are provided for all species and subspecies recognised.

Evidence is limited, but *Gentianella* appears to have arrived in New Zealand from South America once and has probably dispersed once from New Zealand to Australia. The place of the first establishment of *Gentianella* in New Zealand appears to be in the southern half of the South Island. An initial radiation in the lower South Island was followed by northward range extensions and dispersal events. A second radiation occurred in the Nelson and Marlborough mountains.

Keywords

Gentianaceae; *Chionogentias*; *Gentiana*; *Gentianella*; *Oreophylax*; New Zealand; Australia; South America; Australasia; biosystematics; taxonomy; classification; relationships; new species; new combinations; new subspecies; biogeography; origins; ultramafic; edaphic; limestone; calcicole; modes of speciation; parapatric speciation.

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Statement of author's intentions

This thesis does not fulfill the requirements of effective publication in the Botanical Code of Nomenclature (Greuter et al. 2000). Anyone may adopt its recommendations (e.g., for the use of the name *Gentianella* for the New Zealand gentians), but cannot use any of the new names, new combinations, or lectotypifications proposed here. The systematics section is presented here "as if" it were presenting new names, combinations and typifications for ease of comprehension. These names, combinations and typifications will be published separately. There may be changes to the classification adopted here as the result of the review process.

INTRODUCTION

Overview

Taxonomic revisions of genera are the most common way in which our taxonomic knowledge of the biota is updated and improved. Such revisions provide the brickwork of our taxonomic knowledge. A full generic revision examines a genus in its entirety, and rationalises the case-by-case decision making of single publications of new species that often results in inconsistency and duplication in the classification. A revision that is limited to the part of a genus in one country imposes some limitations on this process but is a contribution towards a complete generic revision.

This work is a country revision of *Gentianella* for New Zealand. A thesis provides an opportunity to examine the methods and principals of a subject. In the case of taxonomic revisions, these issues are:

Firstly, issues to do with the criteria for recognition of taxonomic units at various levels, particularly at genus, species, and infraspecific levels. These criteria are determined by conceptual issues over what are natural or artificial units (called taxa), what are the relationships between these units, and what aspects of the relationships should be expressed in the classification.

Secondly, issues to do with the kinds of evidence that are used in devising a classification. The main source of information is the plants themselves, and this provides information from gross morphological, microscopic, and submicroscopic features. But a second distinct source is biogeographic information from the distribution of the plants, mainly taken in conjunction with knowledge of the history of the earth's surface, but also valuable on its own to assess the degree of reproductive isolation caused by separation in space.

Thirdly, there are issues of how this evidence is interpreted: (1) Phylogenetic interpretation, and how this influences or should influence the classification. Is it desirable the classification reflects this, and if so, which aspects of the phylogeny should be reflected, and how? (2) How should life-cycle, breeding systems, pollination biology, degrees of interfertility, ecological factors influence the classification? (3) Methods of analysis of morphological evidence. These can be grouped into quantitative methods of analysis, both phenetic and cladistic, and intuitive methods of analysis. They vary in explicitness, objectivity, and effectiveness in uncovering relationships. These methods may not operate at all levels with the same degrees of success.

These three kinds of issues (over taxonomic units, kinds of evidence, and interpretation of evidence) are now introduced in more detail.

Taxonomic units

The appropriate generic position of the group under study is often in question. Where a complete world revision is being done, the position and boundaries of the genus in its wider context need to be examined. Methodological issues exist over what is a genus, what the criteria for a group of species being a genus should be, and in what circumstances should a genus be divided into several smaller genera? A trend toward better definitions and criteria, and more thorough and explicit forms of taxonomic analysis has raised new problems here, the most important one being the questions of the importance of monophyly and paraphyly. The author of a revision needs to understand the history of views on this subject and current thinking on it. This is particularly so since the criteria for recognition of a genus are so poorly specified. It is still the case the consensus of taxonomists determines what should be regarded as a genus, not the consistent application of a set of objective rules.

Similar methodological issues exist over what is a species. To what degree are they natural units? What are the criteria for their recognition? This issue became an important one in the middle of last century with the increase in use of quantitative methods and the increase in the understanding of evolution in biology. It continues to be perhaps the most important issue within taxonomic methodology. The author of a revision needs to be aware of these issues, and look at how they apply to the group under study.

What units below species level should be recognised, and on what criteria? Again, the consensus of taxonomists working in a larger group, or in a country has a major bearing on this, and an author of a revision needs to be aware of the history of, and current taxonomic practice, both in the genus being revised and in wider contexts.

Kinds of evidence

Traditionally in vascular plant taxonomy, the gross morphological features of plants were the ones used to construct classifications. During last century, it became common to supplement these features with microscopic ones, and in some cases, genera have been erected based on microscopic features such as the features of anther wall cells, and chromosome number. Late last century, an entirely new source of sub-microscopic characters became easily available with the invention of the polymerase chain reaction, DNA sequences. The use of DNA sequences as sets of taxonomic characters has within a

decade transformed the appearance of biological journals. DNA sequences sometimes offer better possibilities of estimating phylogeny than morphological characters, and this is now having a strong influence on the methodological issues mentioned above at genus and species levels. There are still limited numbers of regions of DNA for which universal primers exist, and these tend to have the variability that is most useful for phylogenetic analysis of genera and groups of species within genera.

For the revision of a genus, it is helpful to examine what kinds of microscopic characters have been found useful in the genus to date, and to attempt to extend this by examining new sources of microscopic characters. By their nature, they are time-consuming to examine and a commitment of effort is required in order to test their usefulness in the genus.

The geography of plants, that is, their regional and altitudinal distribution, the substrates they occur on and the plant communities they are found in are factors that are sometimes underestimated as a source of information on a species parallel to morphological characters. They are important in deciding the degree of reproductive isolation.

Biogeographic questions require sound taxonomic knowledge, and the revision of a genus often makes available new evidence for answering these questions. Examples of such questions are: how often, by what means, and over what distances has dispersal taken place? How rapidly does a new and distinctive flora evolve in a region, and what are the conditions that promote rapid radiation of species in a genus? Are the important influences isolation of populations, different soil and rock types, or other habitat differences? How constrained is the evolution of a plant genus by its existing habitat preferences, adaptation to availability of pollinators, and basic parameters such as height and lifespan?

These biogeographic issues are, on the whole, ones to be examined after a genus revision. The author of a revision is in prime situation to examine these issues, because of the intimate knowledge of a genus the revision requires.

Interpretation of evidence

Traditionally, classifications were made without the use of, or presentation of explicit analyses of what we now call data. Data in this case is information on plants stored in a structured and uniform way. The advent of computers has made it easy to store and analyse data. As well as statistical analysis programs that do standard procedures such as cluster analysis and principal components analysis, there are now computer programs such as Paup* (Swofford, 1998) written specifically to handle taxonomic data.

Although these changes in technology started 40 years ago and became widespread 10–20 years ago, and the majority of taxonomists are now using these methods, less well resolved are the issues of how the various methods of analysis and their interpretation should influence the classification process.

Perhaps the biggest issue in biological taxonomy has been created by the possibility of reconstructing phylogenies of groups of organisms. Since the rules of classification that are embedded in the codes of nomenclature (e.g., the Botanical Code of Nomenclature — Greuter et al. 2000) pre-date the confident reconstruction of phylogenies, these rules of nomenclature are not primarily designed to express phylogenetic relationships. There is no agreement in the world botanical community as to how much of, and what kind of, phylogenetic information should be expressed in the classification. This issue is particularly acute at present over the question of paraphyly.

By contrast, the use of standard statistical analyses and tests on taxonomic data is uncontroversial. These methods were mostly devised in the early 20th century before the advent of computers, but taxonomists have been slower to adopt them than other biologists. Taxonomists presenting revisions are not usually explicit about their methods of measurement and sampling procedures. The exception to this is in the newer area of phylogenetic analysis where full statistical testing and explicitness about methods are expected. It is as if the traditional aspects of taxonomy, in particular the preparation of keys and descriptions, are considered to lie outside of the scientific method.

Lastly, in addition to morphology and its variation, information on life-cycle, breeding systems, degrees of interfertility, pollination biology, and ecological factors are important to the taxonomist in devising a classification. These sources of information on the biology of organisms were emphasised by the movement called "new systematics" proposed by Julian Huxley (Huxley 1940). Most taxonomists consider these biological factors to be of great importance, but their relative importance depends on how accessible this kind of information is (which varies a great deal between groups of organisms), and how thorough the revision is. Some of this evidence can be gained by first-hand knowledge of the organisms in their habitats, and is a reason why such field knowledge is still invaluable despite the existence of methods like DNA sequencing. A further kind of knowledge that is useful to a taxonomist revising a group is familiarity with the biogeography and ecology of other similar groups of organisms. For the New Zealand plant taxonomist, there is a great deal to be learnt from existing revisions of plant genera on matters such as the principal factors causing speciation in the New Zealand flora.

Part A. Taxonomic revisions, biogeography, and the New Zealand alpine flora

Revisions and monographs

A taxonomic revision considers all named species in a group, and any unnamed candidate taxa that are known about before the study or appear in the course of the study. Davis & Heywood (1963) distinguish between monographs and revisions. A monograph synthesises all that is known about a group, while a revision gives less detail and confines itself to taxonomic and geographical information. Revisions may be done on a regional basis, whereas by implication, a monograph is not restricted to a region. The object of a revision in their view is, "to delimit the taxa clearly (particularly species), to group them in a natural manner and to provide means of identification." (p. 293)

In a revision, descriptions may be short or even absent if a good key is provided. It must take into account the names of all the taxa, and any that cannot be adopted or synonymised must be cited as belonging to taxa of uncertain status.

A monograph, in their view, goes beyond these limited aims. It will attempt an evolutionary interpretation, usually in the light of combined morphological, geographical and cytogenetic data. The introductory parts of a monograph that discuss these data and their interpretation is often the most interesting part of a monograph. Descriptions are essential, and specimens must be cited, making it clear which specimens have been examined. Particularly, all types must be accounted for, and earlier synonymy should not be taken on trust. Gaps and lack of knowledge should not be concealed, rather, they should be emphasised for other workers. Finally, they cite Raven's (1962) statement that the work should make interesting reading.

The genus concept

Opinions have gradually shifted over the last 200 years as to whether the genus is a natural unit. Anderson (1940) found that most monographers regarded genera as more natural than species. Mayr et al. (1953, p. 59) expressed the view that, contrary to species,

"The delimitation of the genus is subjective. Most genera (particularly the monotypic ones) could be united with other genera, and most polytypic genera could be subdivided equally well into small genera. Where the limits of the genus should be drawn in any given case is left to the subjective judgement of the individual worker."

Wiley (1981, p. 72) believed that supraspecific taxa are natural, arguing that a natural taxon is "a taxon that exists in nature independent of man's ability to perceive it". Wiley appears

to be arguing that natural taxa are monophyletic groups. Not all taxonomists use "natural" in this way. Stuessy (1990) thought that genera are less natural than species and that they represent a discontinuity in nature. Stuessy's thinking on this is clearly influenced by the phenetic view in which the size of the gap between groups of species is the main criterion for their recognition as genera.

Judd et al., (1999) say that "Ranks are arbitrary", reflecting a view that has become more prevalent with the increasing number of phylogenetic trees appearing in the literature. Trees based on DNA sequences show continuous variation in the branch lengths that separate supraspecific taxa, weakening the perception that there are any natural levels at which groups appear above species level.

To some the problem is created by the fact that the levels of family and genus are compulsory under the present International Code of Botanical Nomenclature. Those who advocate a phylogenetically-based code" (Cantino et al. 1999) take the view that only the species rank is "natural" and that names above species rank should be created wherever there are enough shared features to define a group, but none of these higher ranks should be compulsory. The Phylocode proposal (Cantino & de Queiroz, 2001) has been written by cladists who wish to retain the species rank as the only compulsory rank. Few taxonomists appear to agree with the view of Mischler (1999) and Pleijel (1999) that there should be no compulsory ranks.

Judd et al., (1999, p. 28) accept monophyly as a basic requirement for a genus and give four criteria for deciding which monophyletic groups to name as a genus: (1) the strength of evidence supporting a group; (2) the presence of an obvious morphological character; (3) the size of the group; and (4) nomenclatural stability. The size criterion is difficult to state, but Bentham (in an unpublished manuscript cited in Stevens 1997), stated that genera should be large, consisting of between 10 and 100 species. Kelch (2002) points out that this reflects the view at that time that taxonomic groupings were largely made for reasons of convenience, an aid to memory. Kelch (2002, p. 32) believes "Such considerations are not irrelevant today. Genera and other higher-level groupings should indicate relationships between taxa. Grouping that are too small (monotypes) and too large obscure phylogenetic structure."

Another way to approach the problem of how to make grouping at genus level is by acknowledging that since every named species already belongs in a genus, the least disruptive way to work at present is by careful remodelling of existing genera. Stuessy (1990, p. 203) uses this approach by discussing recommendations made by McVaugh

(1945). McVaugh's eight recommendations were: (1) that special consideration be given to qualitative morphological characteristics; (2) that the recognition of segregate genera based on minor or single characters should only be allowed in particular instances to preserve usage; (3) that the biological unity of a genus is more important than the gap between it and its close relatives; (4) that generic limits should only be changed after a full study of variation within the complete range of the group; (5) that decisions on whether to establish segregate genera should be based on the relationship of the segregate to its core genus, and not the relationship to other segregates; (6) that segregate genera should be sharply delimited, and intermediate species should be left in the larger genus; (7) that the strength of the argument to segregate genera varies proportionally to the number of differentiating characters; (8) that a distinctive geographic range is a strengthening feature for a segregate genus.

Some explanation of the terms and concepts in these rules seems required. The third statement mixes a biological criterion, presumably something like a shared character which is of biological importance, with a phenetic criterion, the distance from a group of species to any other group of species. This mixture of criteria would make this rule a difficult one to implement.

A core genus is an old large genus from which some genera have already been segregated and which contains some potentially distinct species or groups of species that could be split from it as segregate genera. Usually these segregate genera will be smaller than what is left of the core, but it could be the case that the core left after remodelling is smaller than any segregate.

A minor character is a character which in the context of the family, tribe, or genus, is one that shows variability, seems to be artificial in its definition, or shows homoplasy, and so is rated as having low value for discriminating a genus, as its use as the basis for a classification is likely to result in polyphyly in the genus.

Stuessy (1990) raises the point that the practical aspect of such remodelling of genera needs to be considered. The number of new combinations needed in such changes is a consideration. An alternative which allows the expression of evolutionary relationships without creating "nomenclatural burden" is to make subgenera, sections, and series. Because these ranks are not documented in indices such as the Kew Index, and less formal published work (e.g., floras and field guides), not to mention the memories of botanists, reclassification at these levels do not result in such extensive changes in usage.

Stuessy (1990) finally points out that remodelling of genera should only be undertaken when an entire genus is understood.

Davis & Heywood (1963, p. 103) take a rather different view to Stuessy. Their recommendations can be summarised thus: (1) The genus should be natural. By natural, they mean "based on overall resemblance". (2) Overall resemblance should be used in drawing lines between closely related genera. This appears to be essentially the same as their first point. (3a) Differences should not be small or inconstant. (3b) Genera should be consistent with others in the family in their degree of difference. (3c) The size of the gap between genera should be inversely proportional to the size of the groups. That is, large groups can be separated by small gaps. (3d) Remodelling of genera should be minimised because changes are a nuisance. In addition, Davis & Heywood point out that suitable generic characters are often adaptive ones, for instance floral characters that are determined by a mode of pollination.

Few authors of taxonomic manuals (e.g., Stuessy 1990; Davis & Heywood 1963; Mayr et al. 1953; Simpson 1961) are specific on what kinds and numbers of differences between groups of species are sufficient to warrant genus recognition. Winston (1999, p. 341) is an exception. She says "Genera are defined not by one character, but by a group of carefully chosen characters. Usually at least some of them are correlated either functionally or genetically and so are present in all the members of the groups. The members of a genus do not have to share all characters, however. One or more species in a genus may lack one or more of the diagnostic characters, or may have a character present but in a modified form."

Judd et al. (1999) in their second criterion for recognising a group of species as a genus ("the presence of an obvious morphological character") are making the universal presence of a character state a requirement, whereas Winston (1999) seems to be of the view that a defining character state need be shared only by most species.

The species concept

Initial species concepts in the early period of scientific botany of Linnaeus, Ray, and Cuvier were influenced by the Aristotelian distinction between essential and accidental properties of things, a view that saw variation between individuals as unimportant. The properties of species for Linnaeus were: distinct, immutable, and true-breeding (Ramsbottom 1938).

Later in his career, Linnaeus developed a theory of speciation by hybridisation. This theory persisted for some time amongst botanists uncomfortable with Darwin's theory of evolution. It was still influential last century in New Zealand among botanists such as Cockayne and Allan who were influenced by Lotsy, who visited New Zealand in 1925. In his book "Evolution by means of hybridisation" (1916), Lotsy subscribed to the Linnaean view that

"... hybridism is the only source of variation useful for evolution and discarded the idea of mutation ("transmissible variability")" (Godley 1979, p. 213).

Hooker in the *Flora of New Zealand* (1864, p. xxiv), gave a species definition taken from Bentham: "all the individual plants which resemble each other sufficiently to make us conclude that they are all, or may have been all descended from a common plant." This monophyletic-group definition fails to give sufficient conditions for determining whether a set of plants constitute a species rather than some other taxonomic unit such as genus or variety. However, the definition is a very good one in that it combines both a morphological basis (resemblance) and an evolutionary basis (common descent).

Darwin, according to Mayr (1957, p. 4), considered that species didn't essentially differ from varieties in anything more than degree of difference, because evolutionary change is gradual and continuous. Mayr quotes Darwin expressing the opinion that "In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow".

We owe to Mayr the explicit formulation of a species concept that attempts to make the species rank a natural, non-arbitrary one that avoids a slide into the unsatisfactory definition of Darwin. Mayr defined a species as a group of interbreeding populations (Mayr 1969). There should be less variation within a species than between species, because interbreeding creates uniformity. A barrier to interbreeding is an evolved feature of an organism that helps maintain its distinctive gene combination that is adapted to the environment in which it occurs. Mayr's biological species concept gained widespread acceptance for many years, and was defended by some botanists (e.g., Grant 1971) despite its limitations in the plant kingdom where hybridisation between species is more common than among most animal groups.

There are three main problems with the application of this concept. Firstly, a practical difficulty of knowing to what degree populations are interbreeding, or conversely, reproductively isolated. Secondly, how to apply the concept in non-outcrossing taxonomic groups. Thirdly, the biological species concept is not applicable to allopatric taxa, taxa that are reproductively isolated by geographical barriers. These are particularly common in island archipelagos. To cope with the island situation, Mayr (1942) supplemented his species concept with several ad hoc rules: firstly, using the dictum "if in doubt lump", that is, he recommended recognising subspecies rather than species for related taxa of each island. Secondly, he argued that the decision on whether to recognise an allopatric species or subspecies should take into account what might happen if there was contact between island taxa, i.e. whether the taxa would maintain their distinctness or lose it. Thirdly, he

suggested that the degree of morphological difference between sympatric species can act as a guideline to evaluate allopatric forms.

Sympatric outcrossing species, in theory at least, present fewer problems. As Stuessy (1990, p. 190) says, "if morphologically distinct population systems are completely overlapping, they are probably reproductively isolated and hence best viewed as good species." It is believed by most taxonomists and evolutionary biologists that a barrier of some kind that divides a species for a time is necessary for the initial stages of speciation to occur, and that the barrier is usually geographic. Subsequent meeting of sibling species results in selection for some kind of incompatibility, usually pollen-stigma incompatibility. The mechanism of this is usually supposed to be that hybrids are less successful because they have lower fertility and may be less well adapted to their environment than the parent species. As a result of lower reproductive success, a gene for incompatibility will be a successful one in a newly formed species. If such barriers to crossing do not form, one must assume that the existence of two interfertile sympatric units is temporary.

Since Mayr's contribution, there has been no entirely new species concept which avoids the problem of arbitrariness in the species rank. The ecological species concept of van Valen (1976) is a variant of the biological species concept in that it characterises species as units maintained by uniform selection pressures from the environment rather than by interbreeding. This species concept fails to establish the species as a non-arbitrary rank as its proponents do not argue that environmental niches are discretely different from each other, and it is doubtful whether such an argument could be convincingly made. The most recent species concept that has gained some acceptance is the phylogenetic species concept (Cracraft 1997). This is a restatement of the biological species concept in that it marks the boundary between species and subspecific taxa as the point at which interbreeding ceases. This species concept has the same problems that beset the biological species concept (determining reproductive isolation, non-outcrossing types, and how to deal with allopatric taxa). The minimum diagnosable species concept (Judd et al. 1999) does not manage to avoid the problem of arbitrariness in the rank of species, and its application would seem to necessitate raising all infraspecific taxa to species rank, without any real justification.

Ehrlich & Raven (1969) did not believe that the biological species concept could be used in plants as it requires substantial gene flow between interbreeding populations, and that the evidence for this gene flow was lacking in published studies, mostly ones involving crop plants. This conclusion was backed by more thorough subsequent reviews of the evidence of pollination distances and genetic variation between populations (e.g., Levin 1981) and it has become widely accepted that there is insufficient gene flow between

populations to maintain most species. Some plant biologists have concluded that the real biological units are populations rather than species ("Local populations or metapopulations would presumably replace species as the unit of evolution" — Rieseberg & Burke 2001, citing Levin 2000 and Luckow 1995). These populations units are on such a small scale that their recognition as species would be impractical.

Rieseberg & Burke (2001) have recently given the biological species concept new credibility by arguing that gene flow can unify populations even when rates of gene flow between populations are low if the strength of selection pressure is high enough (where the selection pressure, $s > 0.05$). They also argue that occasional long-distance dispersals (of pollen or seed) greatly enhance rates of spread of genes between populations, and that these long-distance dispersal events have not been taken into account by biologists modelling and measuring rates of gene flow. They also make the point that the time available for gene flow to act as a cohesive force in species is very long because of the slowness of the rate of speciation. In selfing species, they say that gene flow levels are not high enough to prevent local differentiation due to genetic drift, but that species cohesion only requires collective evolution of a small number of genes, not all. Since species are usually characterised biologically and taxonomically by qualitative characters that are due to one or a few genes, only these need to be maintained by gene flow to ensure uniformity within species, and lower levels of gene flow are needed for this than to maintain uniformity in all genes.

Species concepts applied to the New Zealand flora

Most of New Zealand's flora was named in the period from Hooker's visits to New Zealand and the 1950s when the last of the "regional botanists", Simpson and J. Scott Thomson, published their new names. Authors such as Kirk, Cheeseman, Cockayne, and Petrie did not speculate on their species concept with the exception of Cockayne, who had a strong theoretical interest in evolutionary theory and autecology.

Cockayne (1917) saw that Hooker's species definition of 1864 is insufficient to determine what should be regarded as a species. Cockayne believed that there are discernible groupings at a number of levels, and that there is some arbitrariness in what is regarded as a species and what is regarded as a subspecies. He distinguished "biological species" which he believed should be named as varieties, and "taxonomic species" which he believed were aggregates of biological species, and were required for stability and practicality in flora work. Thus, he believed the variety to be an entity of great importance, and that many more varieties should be named as more detailed work was done on the New Zealand flora. This should only be done after intensive study of species in the field and in

cultivation, a task he called "experimental taxonomy".

Cockayne's (1917) view on species group and regional species outlined above was expressed more recently by Heywood (1963) who also distinguished the "aggregate species" and "biological species". Heywood believed that to recognise all biological species at species rank would lead to unrecognisable and unidentifiable species, and that the units recognised at species rank should be the aggregate species. Heywood's and Cockayne's view makes the species a pragmatic and arbitrary unit while recognising that there is a non-arbitrary biological unit too fine to be practically used.

An example of the use of the aggregate species concept is given by Fisher (1965) in his treatment of the alpine ranunculi of New Zealand. In what was probably the first explicitly evolutionary view of change in the New Zealand flora, Fisher said: "There appears no reason why evolutionary changes should not continue today as in the past. ... It follows that any collection of such lines of descent is likely to contain a variety of stages". Fisher found in his group a pattern of continuous variation, which he said is at odds with the rigidly discrete steps of the taxonomist (p. 87). Fisher rejected this as the outcome of hybridisation, but saw it as the outcome of differentiation along geographical lines. He rejected the pragmatic approach of the 75% : 25% rule of dividing species into subspecies or varieties in which 25% of specimens are allowed to be unclassifiable below species level. Fisher's solution was to show diagrammatically the geographical variation in a species and to recognise broad species, e.g., a broadly defined *Ranunculus insignis*, a species that contains previously recognised species such as *R. monroi* of Marlborough.

Raven & Raven (1976) rejected the biological species concept for New Zealand *Epilobium*. They found that in New Zealand, "33 of the 37 native species of *Epilobium* in New Zealand, and in most populations of *E. glabellum*, autogamy is the predominant form of reproduction." (p. 38) In addition, they observed c. 8 species to be cleistogamous. They concluded from this, and from the low numbers of pollinators seen visiting most species that, with a few exceptions in the taller species, gene flow within populations is very limited, and gene flow between populations even more limited.

This view was in accordance with the view expressed in Ehrlich & Raven (1969) that the biological species concept is not useful because gene flow is generally more limited than Mayr's concept requires. Raven & Raven (1976) were impressed by the diverse habitats in which New Zealand *Epilobium* species are found and believed that species were being maintained by uniform habitat selection pressures. In taking this view, they were adopting what became known as the ecological species concept. In this view a species throughout its range occupies a single niche. Because of this, all individuals of a species experience the

same selection pressures and this maintains uniformity in the species. This uniformity is maintained despite a lack of gene flow across the range of the species (van Valen 1976).

In Raven & Raven's view, distinct morphological non-outcrossing species can be recognised as easily as outcrossing species. However, since such species are recognised by their morphological and habitat distinctness, the problem arises as to how specific and infraspecific ranks may be applied.

Their discussion of the three subspecies they recognised within *Epilobium alsinoides* is the best illustration of their approach to this. The three subspecies are "sharply distinct" in the North Island, but not in the South Island. Two of the subspecies are cleistogamous and all are autogamous, but they see evidence of occasional hybridisation, particularly in the induced tussocklands below the alpine zone. Within *E. alsinoides* subsp. *alsinoides*, they describe a complex pattern of geographical variation including sympatry of two subspecies on Banks Peninsula, Nelson Lakes and on the Chatham Islands. They say about this situation, "It is not unusual for two or more forms of the same species to occur sympatrically among self-pollinating organisms, and their sympatric occurrence is not connected with the sympatric occurrence of outcrossers such as the birds that were chiefly stressed by Mayr (1942, p. 187) when he clearly outlined the importance of sympatry in making taxonomic decisions: "... Botanical taxonomists are just beginning to realize that subspecific recognition may be appropriate for partly sympatric, partly intergrading entities in autogamous groups."

Epilobium alsinoides subsp. *tenuipes* is distinct from the other two subspecies in the North Island and upper South Island, but further south shows continuous variation between two extremes, and cannot be clearly distinguished there from subsp. *atriplicifolium*. *E. alsinoides* subsp. *atriplicifolium* varies in its form with altitude, but also has a scattered geographical variant that resembles subsp. *alsinoides* except for its smooth seeds. They attribute this variation pattern to local introgression with *E. glabellum*, *E. hectorii*, and subsp. *tenuipes*. They summarise the situation by saying that it would be possible to recognise either a single highly variable species, or a large number of small and relatively uniform entities. They take a middle course of recognising three subspecies. They have two hypotheses as to how the situation arose: either that subsp. *tenuipes* was a distinct and widespread autogamous species which lost its distinctness in part of its range by crossing with subsp. *atriplicifolium* as a result of the disturbance of the South Island montane tussocklands, or that subsp. *tenuipes* was an autogamous race with a well adapted and uniform element that spread into the North Island.

It is clear from such an account that the taxonomic decisions in such a group are to

some degree arbitrary, and are an attempt to reconcile a complex and only partly understood pattern of variation with the practical needs of classification. The Ravens wished to give some recognition in the classification to variation that exists within a species, but did not wish to name every geographical variant encountered. This taxonomic dilemma and its postulated causes (lack of barriers to hybridisation, introgression with other species to produce localised variants, disturbance of habitat, range expansion of a localised variant, altitude-based variation) is one commonly met with in the New Zealand flowering plant flora.

Heywood's fears expressed in 1963 that the adoption of a biological species concept would lead to a proliferation of unrecognisable species do not appear to have been realised in New Zealand. One source of such a proliferation would be the recognition of each ploidy level in species in which more than one level is found. The large number of chromosome counts now obtained for the vascular plants (Dawson, 2000) has not translated into many more species distinguished by their ploidy level. However, this may be because of a lack of taxonomic work in the flora more than from a hesitation to name species on the basis of their chromosomal complement.

The use of a biological species concept instead of an aggregate concept is difficult to detect in the New Zealand literature, but it can be most clearly seen where varieties are raised to species rank. The best example is that of the raising of *Hebe salicifolia* var. *paludosa* Cockayne to species rank by Norton & de Lange (2000). This species they believe arose recently by autopolyploidy from *Hebe salicifolia*. This example is clearly one in which Cockayne used the rank of variety for a biological species that is part of a larger aggregate.

Modes of speciation

Sympatry, according to the Concise Oxford Dictionary (Thompson, 1995) means "occurring within the same geographical area". The problem with this definition is, on what scale is the "area" being talked about. As White (1978, p. 277) says, "In the strictest logical sense no two populations can be said to occupy precisely the same area, in the sense of being identically distributed in space". Rivas (1964, cited in White, 1978, p. 227) proposed that the term sympatric be used for species that have "the same or overlapping geographic distributions, regardless of whether they occupy the same macrohabitat..." and proposed the term syntopic for sympatric species occupying the same macrohabitat, i.e. those that are "observable in close proximity and could possibly interbreed." White (1978) points out that cases where separation of macrohabitats preclude the possibility are not interesting, and that

Rivas' distinction has not gained acceptance. White (1978) prefers to define sympatry as follows: "We shall regard two populations as sympatric if their ranges overlap in such a manner that intermating could occur with a genetically significant frequency, unless prevented by genetic isolating mechanisms of some kind."

This definition is written in terms of breeding behaviour and pollination syndromes, as the potential for cross-fertilisation is the issue at the core of sympatry. The problem with such a definition is that it is tied closely to theoretical concepts such as the biological species concept, and makes it difficult to discuss such issues outside of such a theory. It is also difficult to prove, so that most cases of sympatry would have to be referred to as 'possible sympatry'. For these reasons I prefer a theory-neutral geographical concept, and will use sympatry in the sense given by the dictionary cited above. What needs to be born in mind is that the scale of the area shared is very important. Sympatry at the scale of 100 km is very different from sympatry at the scale of 100 m because of limits to pollination distances.

In plants, chromosomal change, geographical isolation, movement into new habitats (e.g. new plant communities, new physical environments, climatic and soil types) are all recognised as important ways in which speciation occurs. Polyploidy has produced as many as 70% of species in some plant groups, e.g. grasses (White, 1978, p. 274). But in most plant groups, geographical isolation seems to be the most important process causing speciation. This is the model of allopatric speciation preferred by most biologists, and strongly influenced by the views of Mayr (1957). Two types of allopatric speciation have been distinguished (e.g., by White, 1978, p. 16). Firstly, where a continuous population is divided by a newly formed barrier such as a sea barrier and divergence of the isolated populations follows, the favoured mode of speciation of vicariance biogeographers. Secondly, where a new isolated population establishes after dispersal. These two types differ significantly in that in the second usually involves a 'genetic bottleneck' which may speed up the rate of genetic change immediately after establishment.

Until recently, there has been widespread skepticism over sympatric speciation, the consensus being that it is "unproven" (e.g., Grant, 1971, p. 222) except for special situations. The two situations in which it has been established involve fish speciation in lakes (e.g., Schliewen et al. 1994), and insect parasites with narrow plant host preferences (e.g., Bush 1969). Maynard Smith (1966) analysed the conditions under which sympatric speciation might occur. Maynard Smith's model was two gene model, and very strong disruptive selection pressure and linkage of the gene for the somatic trait under disruptive selection and the gene for reproductive isolation seemed required. (Disruptive selection is selection

against intermediate forms). Recently, the conditions have been re-examined for sympatric speciation in animals using a multiple gene model. Computer simulations show that environmental conditions can produce bimodal distribution in a character trait such as animal size, and assortative mating is involved (Kondrashov & Kondrashov 1999). Kondrashov & Kondrashov demonstrate two multi-gene models that result in sympatric speciation. In one there is a slight pre-existing linkage of the somatic trait genes and mate preference genes. In the other, there is no linkage but stochastic variation in genetic composition allows selection of individuals in which the linkage occurs. Kondrashov & Kondrashov conclude from their modelling that sympatric speciation is made more likely when the ecological character trait(s) for which there is disruptive selection must result from at least several gene loci, and reproductive isolation must be due to few gene loci.

There are no examples reported in the literature yet of sympatric speciation in plants. The barrier to doing this is likely to have been the difficulty of finding convincing examples where it can be proved that sympatry of sibling species is not the result of a change in geographical distribution of the sibling species after speciation. Armstrong (pers. comm. 2001) claims that this has occurred in five alpine *Ranunculus* species that form a monophyletic group on Mt Kosciuszko and has done hybridisation and transplanting experiments to demonstrate this, but this work has not been published. Armstrong's case depends on an acceptance that the alpine area of Mt Kosciuszko has not changed significantly during the period in which these buttercups have speciated. Armstrong (pers. comm., 2001) believes that the term 'sympatric speciation' is an unhelpful description of his example, but I believe that the model of speciation he proposes, where buttercups have specialised in repeating habitats such as flush zones essentially involves sympatric speciation, and that the simulation models used to demonstrate how this can come about apply to his example. Armstrong found that the alpine buttercups can hybridise to produce fertile F1 and F2 generation and occasionally do in the wild, but that there is strong selection against the hybrids in the wild. This suggests that there is strong disruptive selection but the development of reproductive isolation is not complete.

Parapatric speciation, termed clinal speciation by White (1978), is intermediate between allopatric and sympatric speciation, in that there is contact between the differentiated populations, but it is limited to a line of contact. Where a parent material is responsible for the differentiation (e.g., limestone within an area of non-basic rock), this line of contact follows the boundaries of the parent materials. Objections to this mode of speciation are of the same kind as for sympatric speciation, but it is seen as more likely because of the limited opportunities for gene flow between the populations. Studies have

shown genetic differentiation associated with different parent materials where a parapatric situation exists (Bradshaw, 1952) and has been more widely accepted than sympatric speciation.

Intraspecific ranks and their application in New Zealand

The criteria for use of intraspecific rank have been discussed above under the species concept, but there is also the problem of which intraspecific rank(s) to use. Stuessy (1990) summarises the history of this situation. Initially the term variety was defined by Linnaeus for what we would call environmental forms. The term subspecies originated in zoology but was adopted first by Persoon (1805) for what we would call cultivars, i.e., true-breeding plants derived by selection and propagation from wild stock. Ehrhart (c. 1788, cited in Manitz 1975), used the term for genetically distinct wild populations which are less distinct than species. The Candolles' first Code of Nomenclature of 1867 recommended use of the rank of subspecies for distinct horticultural true-breeding types. During the 1800s, the rank of variety came into use for wild populations that are less distinct than species. This usage was adopted in the Eastern USA and in Britain. In contrast, in the Western USA, Hall & Clements (1923) adopted the term subspecies for the same entities for the reason that they believed there was confusion in the use of the term variety between wild variant populations and variants created in cultivation. A third viewpoint arose in the USA, where both ranks were used, subspecies for broad subdivisions within a species aggregate, and variety for geographically based variants. This third viewpoint continues to have its adherents.

The problem over these categories has part of its origin in a change from an early concept of plant species in which the genetic and non-genetic sources of variation were not well understood and attention was mainly on variation in cultivated plants, to the current situation in which the role of genetic variation and geographical isolation in speciation is agreed on by most taxonomists. Meanwhile, a situation has arisen in which the disagreement is essentially over which term(s) to use, and how many ranks should be used. A lack of a rule or recommendation in the Botanical Code of Nomenclature from its inception has perpetuated this problem. An attempt by Raven et al. (1974) to equate subspecies and variety ranks in the Code failed in 1975. Stuessy's (1990) recommendations on the subject are: (1) to use the rank of form only for variants that need highlighting for some important purpose (e.g., crop plants); (2) to avoid changing subspecies to varieties or vice-versa automatically merely to create uniformity; (3) to use subspecies where no intraspecific classification is in place; and (4) that both categories should be available for

use. Stuessy reports the suggestion that only subspecies be used from a set date, and recommends the year 2000. This has not happened.

In New Zealand variety and form were used for most of last century almost exclusively, in accordance with British practice. Allan was influenced by the views of Jordan (1905) on the sources and types of variation in plants and made use of several terms in his 1961 flora which were recommended at the time: epharmone, meaning an unstable environmental form; jordanon, meaning a species as represented in a region, and used by some taxonomists at this time to replace the terms subspecies and variety because of the lack on standardisation in their use; and linneon, meaning a species complex, i.e., a species over its entire range, with regional variation observable within it.

In Allan (1961), varietal rank is used frequently, and the sole subspecies that appears in the volume was *Callitriche petriei* subsp. *chathamensis* made by Mason in 1959, and presented in Supplementary notes to the flora. As Moore stated in her preface to Allan's 1961 flora:

"infraspecific categories are treated conservatively, only varietal status being recognized; most names were so published and they are recorded without change." (p. x)

From the 1960s onwards, subspecies has been used for the New Zealand flora as the sole infraspecific rank by most authors, for instance by Ornduff (1960) in *Senecio*, Fisher (1965) in *Ranunculus*, Carolin (1964) in *Geranium*, Stone (1973) in *Freycinetia*, Raven & Raven (1976) in *Epilobium*, Garnock-Jones (1980) in *Parahebe*, Orchard (1980) in *Haloragis* and *Gonocarpus*, Edgar (1986) in *Poa*, Garnock-Jones (1986) in *Myosurus*, Orchard (1987) in *Coprosma*, Webb (1987) in *Senecio*, Sykes (1992) in *Macropiper*, and by Petterson (1997) in *Wahlenbergia*.

A minority of authors of revisions of the New Zealand flora in the last 40 years stayed with the tradition of using the rank of variety, e.g., Dawson (1961) in *Anisotome*; Edgar (1966) in *Luzula*; Wardle (1968) in *Pseudopanax*; Nordenstam (1978) in *Brachyglottis*; Gardner (1978) in *Alseuosmia*, and Dawson (1979) in *Aciphylla*. However, in the last 20 years, the only use of varietal rank was by Bayly and Garnock-Jones in Bayly et al., (2000) in *Hebe*, for the reason that the authors were unsure of the distinctness of the taxon (P. J. Brownsey, pers. comm., 2001).

Two New Zealand authors have raised pre-existing varieties to subspecies for uniformity with other newly named subspecies: Arroyo (1984) in her partial revision of *Ourisia*, and Given (1984) in his partial revision of *Celmisia*.

Only two New Zealand authors have used both ranks simultaneously. Lloyd (1972) adopted a two-level hierarchy in his revision of New Zealand *Cotula* section *Leptinella* but

in an unusual way. Geographical variants are treated as subspecies while a single character non-geographical form is treated as a variety. Lloyd's variety is clearly what would be regarded as a form. Connor (1991) also used all three ranks (subspecies, variety, and form) in *Chionochloa*. In *Chionochloa rubra* he recognised three geographical variants as subspecies and within subspecies *rubra* he separated an Egmont population as a variety on the basis of a single character difference.

In summary, whereas in the 19th century and the first half of the 20th century, the use of variety to describe geographical variants was almost universal in the New Zealand botanical literature, the situation is now reversed to one in which virtually all authors prefer to use the rank of subspecies as the sole infraspecific rank.

A recent trend in New Zealand taxonomy has also been the avoidance of the use of infraspecific ranks. A. P. Druce and B. Molloy (pers. comm., 2000) have both held this view. The motivation for this approach appears to be a desire for simplicity, rather than a denial that there are geographical variants showing varying degrees of differentiation (B. Molloy pers. comm., 2000).

Phylogeny and classification

Hall & Clements (1923) in their revision of *Artemesia*, *Chrysothamnus* and *Atriplex* provided what appears to have been the first phylogenetic trees for plant genera in the English-speaking literature. Hall & Clements did not explain how their phylogenetic trees were derived and their classification does not seem to be an outcome of the phylogeny. This may have made their espousal of a phylogenetic view unconvincing to their readers, but at this time, there was no computational method known for deriving trees from character tables. Oliver (1935) adopted a similar approach in his *Coprosma* revision, giving a series of partial phylogenetic trees for the 34 groups he recognised, and an almost fully resolved tree for Hawaiian *Coprosma*. In New Zealand, Allan (1953) rejected the phylogenetic method of Hall & Clements, believing that it rested on speculation, and that one could only describe resemblances and differences, but could not say that taxa were "closely related" to others. The influence of the phylogenetic point of view in New Zealand seems to have diminished over the period following the expression of this view of Allan's until the 1980s. Revisions done in New Zealand in this period refrained from such speculation on the relationships between species coinciding with a period of reductionism throughout the sciences. The exception was Fisher's (1965) revision of the alpine ranunculi which presented a partial phylogeny. Nevertheless, subgeneric and sectional names have always been used to convey relationships, but these higher level taxa were made sparingly by New

Zealand flowering plant taxonomists. Moore made ten informal groups within New Zealand *Hebe* (Allan 1961) and Allan made both sections and subsections in *Celmisia* (Allan 1961).

Not until the devising of the Wagner ground plan divergence method (Wagner 1980), was it possible to derive a phylogenetic tree from a character table. This method was first used for a New Zealand group of plants by Vitt (1983) in his revision of New Zealand *Macromitrium*. As in the case of Hall & Clement's work, the phylogeny was presented as an addition to the revision. It was not until Garnock-Jones' (1993) revision of *Heliohebe* that changes to a classification resulted from a phylogenetic analysis for any New Zealand plant group. Garnock-Jones (1993) used a phylogenetic tree derived from morphological characters to argue for several changes in rank in his new genus *Heliohebe* on the basis of the relative positions of taxa in his cladogram derived from morphological data. He made *Hebe raoulii* var. *pentasepala* a species on the basis that in his cladogram it appeared at the base of a clade of two other species (*H. laudiana* and *H. raoulii*), and that it was sympatric with *H. raoulii*. Since then, it has become more common to revise classifications using phylogenetic evidence. For instance, Mitchell et al. (1997) reinstated *Raukaua* as a genus distinct from *Pseudopanax* prompted by a phylogeny derived from DNA sequences that was presented in Mitchell & Wagstaff (1997) but with supporting morphological evidence.

Changes such as these attract little opposition, but at a more general level, the question as to whether a classification should reflect phylogeny has become an important issue because the view a taxonomist takes on the issue has strong practical consequences for their classifications. The question centres on the problem of paraphyly.

A monophyletic taxon in the broad, non-cladistic sense is a taxon whose species share a specified common ancestor. A monophyletic taxon, in the narrow sense as defined by cladists, is a taxon which contains all species with a specified common ancestor. A paraphyletic taxon is defined as a taxon which contains species that share a specified common ancestor, but not all. A common way to express this is to say that taxon A is paraphyletic by exclusion of taxon B which is nested within it. With few exceptions (e.g., Cronquist 1987), taxonomists have considered that monophyly in the broad sense was an essential property of taxa above species level. However, the taxonomic community is currently split over the desirability of recognising paraphyletic taxa. In particular, whether it is desirable to have a classification that allows nesting of taxa of the same rank, for instance, for a genus to be nested within another genus.

The two contrasting points of view on whether paraphyletic taxa should be recognised relates to a difference in point of view over whether classifications should reflect phylogeny.

Taxonomists such as Brummitt (1997) believe that classifications need not reflect phylogeny, and that the two should be kept apart. Those such as Cantino (e.g., Cantino et al. 1999) believe that classification should reflect phylogeny, that the present rules of classification are an imperfect way to do this, and that they should be changed.

For Brummitt (1997), paraphyletic taxa are acceptable because he holds the view that new distinctive groups of species arise from within existing ones, and deserve the same rank as the genus they originate from. Brummitt believes that to remove all paraphyletic taxa from the existing classification of plants would create huge numbers of changes with very little benefit. Brummitt believes that paraphyletic taxa are an inevitable outcome of the present classification method embodied in the Code of Nomenclature. To eliminate these would require adopting a new code of nomenclature that does not make the ranks of genus, family and order compulsory. Brummitt prefers to retain the present code of nomenclature partly because there is a lack of adequate data on the phylogeny of most taxa, but also because he believes that the present classification system and the rules that govern it work well and should not be replaced. He believes that there will never be sufficient support by taxonomists for a major change in those rules.

The phylogenetic point of view is represented by authors such as Welzen (1997), Cantino (in Cantino et al. 1998), Donoghue (in Donoghue & Cantino 1988) and Quieroz (1996 and in Quieroz and Gauthier 1992 and 1994). These authors share with Brummitt the view that the present code cannot reflect phylogeny adequately, but they believe that a new code is needed to express the phylogenetic information now being gained from DNA and morphological analyses in a classification. Such a phylogenetic code would not make any rank above species compulsory and ranks would not be assigned to names made above species level. The resulting hierarchy would imply that some names were of higher rank than others, but not the form of the names themselves. A conspicuous feature of such a code is that all names would be uninomials, as family and order names are at present.

Welzen's (1997) main objection to paraphyletic groups is that they are assigned the same rank as the group they are nested within when their position in the phylogenetic tree dictates that they should have a lower ranking. For example, monocots are given equal ranking to dicots in the present classification despite it being universally accepted that they are a group nested within the dicots. For taxonomists such as Brummitt, this is not a problem as their distinctness takes precedence over their position in a phylogeny. The difference in opinion between Brummitt and the Phylocode advocates comes down to what a classification should reflect. For Brummitt or Cronquist (1987) it should reflect resemblances, particularly if these resemblances are easily observed and therefore of

practical use. For them, degrees of similarity and distinctness that define taxa are more important for a classification than the expression of relationships. For advocates of a phylogenetic code, the opposite is true. For them, a classification should reflect the evolutionary relationships that are now becoming visible in trees derived from the large numbers of DNA sequences being obtained.

Brummitt (1997) believes that the Linnaean classification and nomenclature will never be replaced. However, if the time comes when the majority of published taxonomic work uses phylogenetic analysis and depicts relationships between species and higher level groups using trees, the view that classification should reflect relationships rather than similarities and the incongruence between the Code of Nomenclature and these phylogenetic analyses may make major changes in the Code seem the preferable option. The fears of Brummitt and others that this will lead to taxonomic instability, or at the worst chaos, may not be justified, just as the fears of Heywood (1963) and Cain (1959) of taxonomic instability resulting from adoption of the biological species concept have not been realised.

Pleijel (1999) provides an example of a revision of a group of annelids done according to a phylogenetic code using Quieroz & Gauthier (1992) as a guide but taking the more radical step of not recognising a species rank. Pleijel's names are invalid under the Zoological Code of Nomenclature and will not be listed in indices, but if enough annelid specialists use Pleijel's names, they may gain a de facto validity.

Cantino et al. (1998) in their revision of *Caryopteris* stayed within the existing nomenclatural rules but adopted a classification they considered did not involve recognition of polyphyletic or paraphyletic taxa. They gave a synopsis of their classification which included phylogenetic definitions of each taxon using the formulation "the least inclusive clade that contains ...". They made several new genera where there was a lack of resolution in their analyses. An alternative which they did not consider was to revise the classification where they had good support for doing so, but to leave unrevised those parts where support was lacking. Phylogenetic analyses will always have such unresolved areas, and a defensible option is that of leaving names unchanged and indicating the need for further work.

While there is no consensus over how to deal with parapyly, a situation likely to persist for the indefinite future, choices have to be made by anyone revising a group and wishing to conform to the Code of Nomenclature. The choices are: (1) to accept existing paraphyletic taxa and make new ones (Brummitt's view); (2) to accept existing paraphyletic taxa, but not make new ones; (3) to avoid recognition of paraphyletic taxa by creating new groups of equivalent rank to those causing the parapyly (the approach of Cantino et al.

1997); (4) to avoid paraphyletic taxa by lumping existing taxa in such a way that the paraphyletic taxa become synonyms (also used by Cantino et al. 1997); or (5) to use methods 2, 3, and 4 within a revision as seems appropriate.

The second option is one that will be followed by many authors, with others adopting the fifth option.

Quantitative methods in taxonomy

A subject that is rarely mentioned in published revisions is how the authors have handled character analysis, data storage, data analysis and the translation of data gathered into species descriptions. The most comprehensive revisions of the New Zealand vascular flora (Fisher 1965, Raven & Raven 1976, Lloyd 1972, Brownsey 1977) did not mention how they compiled their descriptions. Only where phenetic and cladistic techniques are used has it been the practice to document sampling methods and methods of processing data using computers.

Some of the data handling techniques and methods of analysis of taxonomy are peculiar to the subject, but the book title "Statistical techniques in plant taxonomy" does not exist, and the discussion of problems of analysis are only given in terms of experimental biology. Some forms of data handling that are peculiar to taxonomy or more heavily used there than elsewhere are: (1) the coding of characteristics of organisms into characters and character states; (2) recording and analysing a mixture of presence/absence, multistate and quantitative characters; (3) the need to record characteristics of both cultivated plants (for analysis) and wild plants (for descriptions); and (4) the reliance on minimum and maximum values in descriptions and dichotomous keys where most other areas of biology would use mean and standard deviation.

Methods of recording data

There are benefits in using a standardised method of recording data. The data is well labelled and is in a form that can be used for different purposes, re-analysed by another researcher, or by the same researcher at a later date. The only published methods of doing this are the Delta and Lucid computer packages (Dallwitz et al. 1980; Centre for Pest Technology Transfer 1999). Delta generates descriptions, keys, and interactive keys from standardised data sets. Lucid generates interactive keys but does not generate descriptions, but the files are compatible with Delta, and can be converted for description writing. Nexus files are the standard for cladistic analysis and can be converted to and from Delta files. Spreadsheets are used for entering data for multivariate analysis, but can also be used to

record basic descriptive data for several purposes, including descriptions by converting spreadsheet data to Delta format.

Methods of analysing data

Measurements are often taken from cultivated plants grown in the same conditions. This removes the phenotypic component of the variation seen in wild plants. In general, the more sheltered conditions of glass or shade-house will promote larger plants. Measurements from these plants cannot be used for constructing keys and descriptions unless it can be shown that measurements fall within the extremes seen in wild plants.

Whether wild or cultivated plants are used, a common method of comparing sets of specimens is the use of sample means and t-tests to determine the significance of differences in means. Multivariate analysis makes comparisons in many characters simultaneously and in the case of Principal components analysis reduces these to 3–5 variables with the results shown as scattergrams. Cluster analysis uses a similarity matrix derived by comparison of all characters for all samples. The advantage Principal components analysis has over Cluster analysis is that it gives information on the effect of each character on the analysis.

A listing of characters and their states and how they were defined is now standard whenever a phenetic or cladistic analysis is performed. In DNA sequencing studies, a complete listing of the sequences was common in early studies, but now it is common practice to omit the sequences or to show only variable sites and indels in tabular form.

Graphical presentation can make the results of an analysis easier to see and therefore more convincing to the reader. Some methods used are: comparison of means (e.g., Glenný 1998, fig. 8); scatter plots allowing separation using two characters simultaneously (e.g., Godley 1985, fig. 3); bar graphs showing continuous variation (Fisher 1965, Fig. 20; Glenný 1998, fig. 6); tables showing sympatry of species (Fisher 1965, table 22; Raven & Raven 1976, fig. 20); graphs showing hybridisation frequency (Connor 1985, fig. 1); metroglyphs and shape maps (e.g., Fisher 1965, Glenný 1998, Bayly et al., 2000); and silhouettes showing variation (e.g., Drury 1974).

Compilation of species descriptions is usually done "manually", sometimes using a single species description as a template for others. The only alternative that exists is to output descriptions automatically from Delta files (Dallwitz et al. 1993).

Little discussion exists on measurement of plant parts for systematic purposes. Herbarium specimens may not be representative of the wild populations, particularly if the species are at the limit of the size that can be fitted on a sheet. Descriptions are based on adult plants, which could be defined as any plants that are of reproductive age. I have found no discussion in any taxonomic revision I have seen on changes in floral dimensions with

stage of maturity of flowers and I am unable to find any author who restricted their measurements of flowers to a stage of maturity as I have done in this revision.

Biological statistics textbooks invariably deal with measures of central tendency (the mean, and confidence intervals of the mean), and standard deviation as the measure of dispersion of samples around the mean. Taxonomy has an unusual requirement in its use of maximum and minimum values for the purposes of keys and descriptions. Dichotomous keys and descriptions rely on gaps in quantitative characters. Minima and maxima are, of all the statistical measures that can be derived from a sample set, the least well behaved measures. Whereas sample mean, and to a lesser degree sample standard deviation, tends rapidly toward the true population mean and true population standard deviation as sample size increases, minimum and maximum do not. They are dependent on sample size, in that increasing the sample size will eventually result in finding new minima and maxima.

Plus and minus twice the standard deviation from the mean will enclose 95% of samples if the distribution is normal for a character. Deriving maximum and minimum values in this way is appropriate for the "inner" limits. If values encountered during the sampling exceed these values, they should be given as "outer" limits, for instance, $(5-)-8-20(-25)$ mm, where 5 and 25 mm are the smallest and largest values found, and 8 and 20 mm are the figures derived from the sample mean and standard deviation. This was the explicit method of Brown & Braggins (1989) who gave all their ranges in the form $"(5)10\pm3(21)"$ which can also be expressed as $"(5-)-7-10-13(-21)"$ where the middle value is the mean. In practice, I believe few taxonomists derive their inner limits from calculations of sample mean and sample standard deviation. In this revision, I have not derived inner limits in this way because for many species there was insufficient material available to make the standard deviation sufficiently accurate to use in this way. Instead, I have followed the following rule: the observed minima and maxima are set as the outside limits, and the next pair of values as the inside limits, except where there is no real gap between, for instance, the minimum observation and the next-to minimum observation, in which case I have set the minimum as the inner limit and not given an outer limit.

Phenetic analysis

This is the term is used for a multivariate analysis method that involves the construction of a data table of taxa and characters which will be a mixture of quantitative, presence/absence, and multistate. The table is then converted to a similarity matrix using, for instance, Gower's coefficient which handles these various character types in a way that weights them evenly. The similarity table is then used to produce a similarity tree by one of several

algorithms, the best known and most reliable being Neighbour Joining (NJ) and the Unweighted Pairwise Group Method using Arithmetic averages (UPGMA) (Huelsenback & Hillis 1993). Ordination analysis can also be regarded as a part of phenetic analysis. Principal components analysis is an example of this method.

The strengths of phenetic analysis are that it is explicit in its codification of characters, character states, and its analysis method. It uses many samples, and as usually practised, it does not assume species units before the analysis — individual plants are the unit of analysis. Its weakness is that the analysis method does not take account of homoplasy. Phenetic analysis relies on large numbers of characters to overcome the effects of a few unreliable characters (Sneath & Sokal 1973). However, increasing the number of characters may not decrease the percentage of poor characters. Rather the opposite may happen. In my experience, the search for new characters usually results in adding characters which are less satisfactory for various reasons: variability within species, difficulty in coding these as multistate characters, and gaps in the data. Coding of characters is often subjective, but this is true of all formal analysis methods. It is less so in phenetic analysis than cladistic analysis as quantitative characters may be a significant proportion of the characters in a phenetic analysis and do not need to be transformed into multistate characters as in cladistic analysis.

Mayr (1965) makes the point (cited in Stuessy 1990, p. 138) that phenetic analysis is laborious: "gathering and tabulating the information for [analysis] is a very time-consuming operation and is uneconomical when the proper answer is evident to the experienced specialist from a thoughtful inspection of the raw data". Mayr is correct that the information gathering exercise is time-consuming. However, against the extra labour required to do this work must be balanced the benefits that come from the use of an explicit coding and analysis. Most taxonomic decisions made in revisions that predate the use of quantitative methods were made without any or with only limited evidence being given for the decisions made. It is clearer to everyone, the author included, how well supported the taxonomic conclusions are when they result from an explicit analysis. There is the possibility of using the data for other purposes such as automatically generated descriptions and keys, and as raw data for other analyses — now especially common with DNA data. Processing quantitative data is also a much easier job now than it was when Mayr wrote in 1965.

Cladistic analysis

Hennig (1966) is regarded as the originator of the cladistic philosophy, although the phylogenetic point of view has an older origin (e.g., as used in Hall & Clements 1923). Hennig provided a terminology that related to the tree-diagram as a way of visualising

evolutionary patterns. Terms such as autapomorphy, synapomorphy and homoplasy are terms that allow a clear analysis of problems that previously lacked an effective formulation. Perhaps the best example of this is the concept of homoplasy which has replaced the terms "convergence" and "parallel evolution".

Convergence in phenetic terms means similarity in taxa that is not due to their common descent. The term's meaning is inevitably tied to a phylogenetic perspective, as recognised by Sneath & Sokal (1973). Sneath & Sokal (1973) distinguished "overall convergence" of unrelated species, which they considered could mislead a phenetic classification, but claimed that it was rare. "Organ convergence" they thought was more common but posed no threat to a phenetic analysis because the few misleading similarities would be outweighed by non-convergent characters. The term parallel evolution is one whose meaning is not clear, but seems to refer to convergence in closely related species. Sneath & Sokal (1973) admitted to difficulty in finding a definition of the term. Thus, in 1973, there was a lack of an effective formulation for thinking about how mutational change in organisms could be studied and used to reconstruct the evolutionary process.

Homoplasy refers to the independent appearance of a characteristic in more than one place on a phylogenetic tree where the appearance of the characteristic cannot be explained by inheritance of the characteristic by all species with a common ancestor. It is seen most clearly in DNA sequence comparisons because of the discrete nature of the genetic code. Homoplasy in DNA sequences is a frequent outcome of a point mutation happening at a particular site in different species independently. It is evident that mutation occurs more easily at some sites than others, often termed "hot spots" (Hillis et al. 1996). The analysis of DNA sequences has made it clear that homoplasy is almost universally present in DNA and that it presents the major obstacle to the reconstruction of phylogenies.

Homoplasy in morphological data is less well understood. Homoplasy in morphology may be true homoplasy that results from independent "invention" of the same characteristic more than once in different lineages. However, it probably arises more often through the switching on and off of genes that are present in the DNA of all the species that belong to a group, and also by hybridisation and introgression. A source of apparent homoplasy in morphological data arises from coding procedures. For instance, if corolla colour is coded as "coloured" homoplasy in the coloured state may result from the lumping of several colours which each result from a different pigment.

A cladistic analysis algorithm such as parsimony analysis (as implemented in the program PAUP* — Swofford 1998) is based on the idea that of all the possible ways that species can be arranged on the ends of the branches of a tree diagram, the tree or trees that

will give the closest approximation to the true phylogeny of those taxa will be those which minimise the homoplasy. The recognition of homoplasy and an explicit method of constructing an evolutionary tree are the two main strengths of parsimony analysis and the cladistic method.

Other strengths of the cladistic method are that, like phenetic analysis, the coding and analysis is explicit, although not objective where morphological data is concerned, as characteristics of the species must be coded in multistate form. Parsimony analysis, the commonest algorithm used by cladists, has the advantage that it is possible to specify the level of support that exists for particular edges (the lines between nodes) on a tree. It is then possible to draw conclusions from the well supported parts of the tree while disregarding the poorly supported parts. Similarity trees of phenetic analysis do not allow this. Another way to express this is to say that the many trees of the same number of steps that result from a parsimony analysis discourages the view that the "correct" tree is known.

The limitations of the cladistic method are, firstly, that continuously varying morphological data is difficult to incorporate. Methods such as gap coding and overlap coding exist to cope with this but are not widely used or believed to be helpful. This limitation does not affect phenetic analysis. Secondly, the basic unit of cladistic analyses is usually taken to be species, units already arrived at by some previous decision making process. The reasons for this are that below species level, reticulation in descent lines is regarded as an important factor, while above species level it is regarded as unimportant, and that most cladistic analyses and the trees that they produce do not allow for reticulation. Phenetic analysis does not require the units of analysis to be species, and is neutral with respect to reticulation. Phenetic analysis is perhaps most useful at and below species level for this reason, although White (1978, p. 2) thought that "the main utility of phenetic classification would seem to be in classifying the higher categories (genera, families, classes, etc.)." and that "its greatest weakness is its application to species and infraspecific categories". He believed the reasons for this were, firstly, that the method exaggerated the significance of phenotypes, and secondly, that it could not deal with sibling species which exhibit minimal or no morphological differences. The first problem can be overcome by using plants cultivated in the same conditions. The second problem is one which arises in this revision (in the *G. bellidifolia* group), and the results of analysis have to be considered alongside information on distribution and habitat.

There are methods of analysis and graphical representation of relationships that handle reticulation but are consistent with the evolutionary perspective of cladistics (e.g., SplitsTree of Huson 1998 and Lockhart et al. 2001; and Spectronet of Huber et al. in press

and Langton & White 2001) but have not become popular, perhaps partly because of a belief that reticulation only occurs below species level. They can only be applied to DNA sequence data.

One of the major criticisms of cladistics as a philosophy relate to the codification of the tree view of evolution. Cladists have devised rules over how to regard the speciation process and the entities that result from it. At the point where a new species diverges from an existing one, it is said, arbitrarily it seems to me, that two new ones result (visualised on the tree diagram as a dichotomous branching) even though the reality may be that the parent species continues to exist unchanged by the speciation process (visualised by non-cladists as a continuing line with a small side-branch representing the new species). The rules of labelling of tree edges and nodes adopted by cladists appear to be ones where consistency of representation and terminology seem to be more important than representation of what actually happens in different situations where speciation occurs. These rules may have resulted from the fact that many cladists of the 1960s and 1970s were also vicariance biogeographers who had a particular model of speciation in mind.

Biogeography

The distribution pattern of a group of related taxa can make a valuable contribution to the interpretation of the evolutionary history of the group. It is an observable fact that not all species are widespread, implying some limitation on the ability of species or genera to occupy all suitable habitats. How that distributional information is used depends to some degree on some more theoretical questions revolving mostly around the issue of dispersal versus vicariance. Vicariance, as used by some authors, refers to the process of splitting of the range of a taxon by the creation of a barrier within its distribution, and is acknowledged as the main source for speciation by some authors. On a large scale, vicariance events occur when land masses on continental plates move relative to each other, and open or close gaps in previously continuous habitat. In New Zealand, such gaps have been created by changes in sea level and opening and closing sea straits such as Cook Strait, the Manawatu Strait and Foveaux Strait. It is possible that such gaps have also been created by the strong lateral movement along the New Zealand alpine fault. Dispersal, on the other hand, is the extension of the range of a taxon by an organism or propagule such as a seed being moved to a new location, by wind, birds, water or other methods. Undoubtedly dispersal is also an event leading to speciation where the probability of that dispersal event reoccurring is low. If the chances of reoccurrence of the event is high, the newly arrived and established organism will be not have the chance to diverge from the source population and speciation

will not occur.

Cladistic biogeographers such as Humphries & Parenti (1999) have taken the view that whereas vicariance is informative as it can be interpreted from a knowledge of geological history, dispersal is uninformative because the chance events involved cannot be studied and it is best ignored. Sympatry, in their view, indicates dispersal, while allopatry implies vicariance. The term "vicariance" is used by others to refer to sibling species that are allopatric regardless of whether speciation has taken place after dispersal or the breakup of a land mass. I have used the term in this broader sense. Against the view that dispersal is uninformative, van Zanten & Gradstein (1988) showed that dispersal can be meaningfully studied by testing bryophyte spores for their germination rates after subjection to conditions such spores would encounter in wind dispersal. Van Zanten & Gradstein found a correlation between hardness of spores to such effects as freezing and ultra-violet radiation and trans-oceanic distribution and shows that while it may not be possible to study single dispersal events because of their infrequency, it is possible to analyse such events collectively. They called their work "experimental biogeography".

Fossil presence in a region establishes a date by which the taxon must have been present, but does not establish the arrival date, although completeness of a fossil record may give some confidence in this (e.g., Pole's 1994 claim that the New Zealand Tertiary pollen fossil record is very comprehensive). Fossil records are not often equally comprehensive for all regions making comparisons difficult. The fossil record can only be used to establish minimum divergence times, however, these minimum divergence times can sometimes be used to draw useful conclusions. Wagstaff et al. (2000) calibrated their tree based on *rbcL* sequences with the earliest appearance of pollen of the family Apocynaceae in the Paleocene. They then calculated that the two *Tetrachondra* species in New Zealand and South America probably diverged 2.5 Ma. It is now common practice to calculate divergence dates for nodes on DNA trees using average mutation rates, and to give confidence intervals for these dates. The calibration for these is done from the fossil record, or by using the time of formation of new islands such as Tahiti (Crisci & Berry 1990) or the Hawaiian islands (Lowrey 1995).

Where chromosome complement varies, the location of species with the lowest number can be used to establish an area of origin. Trees derived from DNA sequences or morphology can establish the oldest parts of a family or genus and also help locate an area of origin. However, the possibility that a formerly widespread taxon has become confined to a refugium is an alternative explanation.

In the past, areas of high diversity were used as evidence for centres of origin, but

species numbers alone cannot establish this. Large numbers of species in an area are more likely to result from recent radiation than from the presence of a group in a region for a long period. The evidence that is needed to distinguish between recent and old radiations is the presence of gaps that implies sufficient time for extinctions to occur. Interpretation of these contrasting effects is bound to be difficult and provides much less certainty than the kinds of evidence listed above.

Biogeography of New Zealand in the Southern Hemisphere context

New Zealand is one of the best countries in the world in which to investigate biogeographical questions because of its degree of isolation and because of its recent uplift in the last 5 My, resulting in the creation of new environments. These new high altitude environments have resulted in strong speciation, making the alpine flora an ideal one for the study of this process.

The biogeography of New Zealand's flora has mainly been studied from the point of view of its relationship to that of other regions. Du Rietz (1931) believed that *Euphrasia* arrived in New Zealand by land dispersal from South America via Antarctica. The acceptance of continental drift in the mid 1960s by geologists and biologists led to the belief that New Zealand's flora represented a largely unchanged piece of the Gondwanaland flora (Raven & Axelrod 1972). Discussion of this revolved mostly around the genus *Nothofagus*, backed by the finding of fossil *Nothofagus* pollen in Antarctica (Cranwell 1959). Raven & Axelrod (1972) took the view that all Southern Hemisphere biogeography could be explained by continental drift. This initial enthusiasm for a pure vicariance viewpoint was quickly dampened by the realisation that the time of separation, particularly of New Zealand from the rest of the Gondwanan supercontinent 80–100 Ma, was too early to explain many of the flowering plant genera that are in common to regions of the Southern Hemisphere. Raven (1973) modified his earlier strong vicariance viewpoint to a view that the New Zealand mountain flora mainly had its origins in Asia, but was dispersed over oceans via Australia. However, Raven recognised that there was a circum-subantarctic element in New Zealand's flora including *Colobanthus*, *Juncus*, *Epilobium*, perhaps *Euphrasia*, *Ourisia*, *Leptinella*, *Oreomyrrhis*, *Acaena*, and *Uncinia*. Wardle (1978) pointed out examples of dispersal from New Zealand to Australia, and while he agreed with Raven that Australia had been the source of some of the mountain flora, he saw the Pacific Islands as another possible migration route for the Asian flora (e.g., *Melicytus*) and considered that there was also a component of the mountain flora that had a southern pre-glacial Antarctic origin (e.g., *Anisotome* and *Aciphylla*) and another component with a South American origin (e.g.,

Chionochloa and *Cortaderia*). Fleming (1979) saw the New Zealand biota as having Paleoaustral, Australian, Malayo-Pacific, and Neoaustral influences. By Paleoaustral, Fleming meant an old southern flora that evolved in the Mesozoic to early Tertiary that had poor dispersal abilities and included the Proteaceae, *Nothofagus*, the Podocarps, *Aristotelia*, *Laurelia*, *Weinmannia*, *Astelia*, and *Fuchsia*. By Neoaustral he meant a circum-subantarctic element that dispersed to New Zealand on the strong westerly winds and sea currents that arose following the opening of the South America-Antarctica gap.

Most authors until very recently accepted a similar viewpoint to Fleming's, that the New Zealand flora contains an ancient element that has been present in New Zealand since its separation from Gondwanaland, and newer elements from diverse sources. There has been an acceptance of a neo-endemic element to the New Zealand flora involving dispersal across present-day ocean gaps because many of the genera that are in common to Australasia and South America have been shown to have evolved too late to have been present before the separation of New Zealand from Gondwanaland. Lloyd (1985, p. 715) argued that "The large majority of New Zealand plants have arrived by such [long distance] dispersal events at some time during the post-Gondwanaland history of New Zealand ...". Pole (1994) suggested that all of the New Zealand flora was of recent arrival by long-distance dispersal. Brownsey (2001) agreed that for the New Zealand ferns, long distance dispersal since New Zealand's geographical isolation 80 Ma was responsible for most of the flora. McGlone et al. (2001, p. 199) went further than Lloyd and Brownsey and stated that "Most vascular plants reached New Zealand by long-distance transoceanic dispersal, probably during the Late Miocene to early Pleistocene period". Pole (1994), Brownsey (2001), and McGlone et al. (2001) cited changes in New Zealand's climate caused by changes in New Zealand's latitude and global climate changes, and the "Oligocene bottleneck" when New Zealand's land mass was very reduced in area as having had major effects in changing the composition of New Zealand's flora.

There are a large number of genera of flowering plants that are in common to New Zealand and South America. For instance, *Euphrasia*, *Aristotelia*, *Gentianella*, *Nothofagus*, *Gunnera*, *Muehlenbeckia*, *Discaria*, *Abrotanella*, *Ourisia*, *Fuchsia*, *Acaena*, *Colobanthus*, *Rostkovia* and *Juncus*. Most authors have been willing to accept dispersal between South America and New Zealand where species are in common, e.g., *Acaena magellanica*, *Rostkovia magellanica*, *Hebe elliptica* and *H. salicifolia* (Godley 1967). However, the same authors have been unwilling to consider dispersal between the two regions for most of the genera where no species are in common. For instance, Wardle (1978) considered that New Zealand *Myosotis*, *Gentiana*, *Ourisia*, and the alpine ranunculi might have had their origins

in Antarctica.

To summarise, taxa that are in common to South America and New Zealand can have their distribution explained in one of three ways. Firstly, that they are Gondwanan in origin and have been present in New Zealand continuously for 80 My, or arrived over a narrower oceanic gap than exists at present up to 60 Ma, and have been in South America for the same length of time, or arrived from Antarctica to South America no later than 23.5 Ma (Fleming 1978, p. 56). Secondly, that they have dispersed to New Zealand via Antarctica after the separation of New Zealand from Antarctica but before the extinction of the Antarctic flora by the ice cap. This extinction is said to have started in the early Miocene c. 23 Ma (Fleming 1978, p. 60), but was possibly not complete until the Pliocene 5 Ma (Renner et al. 2000). The third explanation is that species or genera in common have been transported directly between South America to New Zealand by some agent, either wind, water, or birds. In this explanation, there can be distinguished two extremes: species which disperse easily (e.g., *Acaena magellanica* with its fruit with barbed spines) and show a circum-subantarctic distribution, and species which have no obvious means of dispersal (e.g., *Hebe elliptica*) and are not widespread in the southern temperate region.

Evidence for the hypothesis that South American species have arrived in New Zealand via Antarctica would be that such groups are likely to have representation on the New Zealand Subantarctic Islands, and that the species there will be older than other New Zealand species. In *Ourisia* the absence of representation of the genus in the Subantarctic Islands counts against the hypothesis. *Hectorella* has been supposed (Fleming 1978) to have had an Antarctic origin because its nearest relation is *Lyallia* of Kerguelen, but it is absent from the New Zealand Subantarctic Islands. In *Ranunculus*, Subantarctic *R. pinguis* is derived from South Island *R. sericophyllus* (Lockhart et al. 2001) and does not support the hypothesis. In *Abrotanella*, the results are ambiguous as to whether the ancestor of the mainly New Zealand clade of nine species that contains the two Subantarctic Island species *A. rosulata* and *A. spathulata* had its origin in the Subantarctic or in mainland New Zealand (Swenson 1997a).

The hypothesis that taxa shared by South America and New Zealand dispersed from South America to New Zealand via Antarctica can be tested by making the extra assumption that those taxa will have dispersed via the New Zealand Subantarctic Islands, a reasonable assumption if the view is taken that the Pacific Ocean between South America and New Zealand is too great a distance for direct dispersal. Two tests can be made for the hypothesis. Firstly, that genera and species present in South America and New Zealand will be also present on the Subantarctic Islands. Secondly, that the Subantarctic species in a

genus will be older than the mainland New Zealand species. Of the 25 genera listed above that are in common to South America and New Zealand, 11 genera are not present on New Zealand's Subantarctic Islands (*Ourisia*, *Tetrachondra*, *Aristotelia*, *Griselinia*, *Gunnera*, *Discaria*, *Euphrasia*, *Nothofagus*, and *Muehlenbeckia*). In addition, *Laureliopsis* of Chile and *Laurelia* of New Zealand do not have a relative on the Subantarctic Islands, and *Dendroseris* of Juan Fernandez Islands and *Embergeria* and *Kirkianella* of New Zealand do not have a relative on the Subantarctic Islands.

Of the 25 genera listed above, 13 are represented on the Subantarctic Islands. These are *Fuchsia*, *Gentianella*, *Myosotis*, *Ranunculus*, *Acaena*, *Luzula*, *Epilobium*, *Abrotanella*, *Hebe*, *Colobanthus*, *Rostkovia*, and *Juncus*. In addition, *Chionochloa* of New Zealand has a Subantarctic species, and the genus may be derived from *Cortaderia* of South America. In order to test the 'via Antarctica' hypothesis, phylogenies are needed for these shared genera to establish whether the Subantarctic species are basal to the New Zealand species. Only in a few cases are these phylogenies available. For *Ranunculus* section *Epirotes*, the Subantarctic species are not basal (Lockhart et al. 2001). The result in *Abrotanella* is ambiguous. More phylogenies are needed to test the hypothesis more completely. However, the absence of eleven shared genera, particularly the herbaceous alpine genera *Ourisia* and *Euphrasia* is significant, but in these two cases, a phylogeny is needed to establish whether the South American species are basal to the New Zealand species.

Hill & Scriven (1995) summarised what is known of the vegetation and flora of Antarctica from the late Mesozoic onwards. In their view, the Antarctic angiosperm flora had its origin in the tropics and may have arrived via Australia. Throughout the early half of the Tertiary, they see the vegetation of Antarctica as having been mixed *Nothofagus* – southern conifer forest which persisted in places until the mid to late Pliocene, although there are doubts about the dating of strata containing the fossils that lead to this conclusion. During the early Tertiary, they see evidence of dispersal via Antarctica both from South America via Antarctica to Australasia and South East Asia (e.g., *Gunnera*), and from Asia to South America (e.g., *Ilex*). Their summary supports the idea of Antarctica acting as a bridge for the dispersal of angiosperms across land, but does not contradict the generally held notion that the separation of New Zealand occurred too early for many of the groups with a Southern Hemisphere distribution to have arrived in New Zealand by land.

Biogeography within New Zealand

Geographical barriers within New Zealand appear to have been important for speciation but no analysis of their relative importance to evolution of the New Zealand flora has been

attempted. The most obvious sea barriers are between the outlying islands and the main land mass of New Zealand, Cook Strait, Foveaux Strait, and a former Manawatu Strait.

The Subantarctic Islands are separated from New Zealand’s main islands by distances of 200–820 km and this is reflected in their overall degree of endemism, 14% at species level (Department of Conservation 1997). The degree of endemism for each island or island group is much lower than this (Table 1), suggesting that dispersal between each island or island group is relatively easy.

Table 1 The Subantarctic Islands of New Zealand, geography and flowering plant endemism.

	Distance from South Island (km)	Area (ha)	Maximum altitude (m)	Endemism in flowering plants
Snares Islands	200	341	152	2/22 species, 9%
Bounty Islands	700	135	88	no vascular species
Antipodes Islands	820	2 100	366	4/68 species, 6%
Auckland Islands	460	62 560	644	5/233 species, 2.1%
Campbell Island	660	11 331	569	2/143 species, 1.4%

The endemic vascular species of the Snares Islands are *Stilbocarpa robusta* (shared with Solander Island) and *Anisotome acutifolia*. The endemic vascular species of the Auckland Islands are *Gentianella cerina*, *G. concinna*, *Plantago triantha*, *Plantago aucklandica*, *Callitriche aucklandica*, and *Poa aucklandica* ssp. *aucklandica*. The endemic vascular taxa of Campbell Island are *Gentianella antarctica*, *Myosotis antarcticus*, and *Craspedia uniflora* var. *subhispidula*. The endemic vascular taxa of the Antipodes Islands are *Senecio antipodus*, *Gentianella antipoda*, and *Senecio radiolatus* ssp. *antipodus*.

Vascular taxa endemic to New Zealand’s Subantarctic Islands but in common to several of them are much more numerous: *Pleurophyllum criniferum*, *Pleurophyllum speciosum*, *Pleurophyllum hookeri*, *Ranunculus subscaposus*, *R. pinguis*, *Cardamine subcarnosa*, *Colobanthus hookeri*, *Coprosma perpusilla* subsp. *subantarctica*, *Anisotome antipoda*, *A. latifolia*, *Stilbocarpa polaris*, *Epilobium confertifolium*, *Acaena minor*, *Damnania vernicosa*, *Abrotanella rosulata*, *A. spathulata*, *Leptinella lanata*, *L. plumosa*, *Myosotis capitata*, *Hebe benthamii*, *Juncus scheuchzeroides*, *Uncinia hookeri*, *Bulbinella rossii*, *Poa ramossissima*, *Chionochloa antarctica*, and *Agrostis subantarctica*.

Of these Subantarctic endemics shared by more than one island group, most are shared by the Auckland Islands and Campbell Island, while it is also common that they are shared by those two places with the addition of Macquarie Island and/or the Antipodes Islands. The endemic flora of these islands tends to be composed of genera that have also radiated in mainland of New Zealand recently, mostly in the alpine zone: *Anisotome*, *Hebe*, *Gentianella*, *Abrotanella*, *Leptinella*, *Hebe*, *Coprosma*, *Epilobium*, *Acaena*, *Celmisia* (as *Damnamentia*), *Senecio*, *Myosotis*, and *Luzula*. It is noticeable from the enumeration above that *Gentianella* species have colonised and speciated more than any other genus present on the islands.

Campbell and the Auckland Islands are volcanoes of Miocene age, while the Antipodes Islands are much younger volcanoes of Pleistocene age.

The Chatham Islands are at a similar distance (c. 800 km) from the New Zealand mainland as the most distant Subantarctic Islands and have a similar degree of endemism. Forty (12%) of the 325 vascular species, subspecies and varieties are endemic (Given 1996), and most of these species have their closest relatives in the North or South Island of New Zealand. For instance, *Hebe barkeri* and *H. chathamica* have as near relatives *Hebe elliptica*, *H. odora* and *H. epacridea*, two species widespread in New Zealand and one an alpine species of the South Island (Wagstaff & Garnock-Jones 1998).

The Foveaux and Cook Straits are narrow barriers c. 20 km wide that formed 3 Ma and 1.5 Ma respectively and were both last bridged during the last glaciation when sea levels were lower (Fleming 1979). Some vicariance (used in the loose sense) caused by Foveaux Strait can be seen. For instance, *Ranunculus viridis* of Stewart Island is sibling species to *Ranunculus sericophyllus* of the South Island (Lockhart et al., 2001), *Leptinella traillii* subsp. *traillii* nearest relative of Southland subsp. *pulchella* (Lloyd 1972), and *Chionochloa lanea* (Connor 1987) is probably sibling species of *C. teretifolia* of Southland (Wilson 1982). The degree of endemism in the Stewart Island flora is 5% (28/580 species — Wilson 1982).

It is notable that no such vicariant pairs are observed at the Cook Strait barrier, although many species are present in one but not both islands, indicating that Cook Strait has been a barrier to dispersal. For instance *Epilobium tasmanicum*, widespread in the South Island and also in New South Wales and Tasmania is absent from the North Island although the Ruapehu area would provide suitable habitat (Raven & Raven 1976). During the Pliocene, most of the lower half of the North Island was submerged (Rogers 1989) and species are absent from the North Island between Wellington and the Ruahine Range that could be expected to be there. Rogers (1989) lists 139 species that are absent from the

lower North Island but occur north and south of the region, although lack of suitable habitat in the lower North Island may account for some of the absences, and the very late appearance of the Tararua Ranges only 200 000 years ago (Ghani 1978) may explain others..

Within the South Island, minor barriers can be seen. The Rakaia Valley appears to have been a barrier to the dispersal of montane and alpine plants, with vicariants *Celmisia spectabilis* var. *spectabilis* and var. *magnifica* north and south of the valley respectively (Given 1984) and *Aciphylla monroi* and *A. montana* north and south of the valley respectively (Dawson 1979), and it is the northern limit of *Raoulia hectori* and southern limit of *Hebe raoulii* and *H. venustula* (Arand & Glenney 1990). In Westland, the Taramakau and Grey River valleys in their lower reaches appear to have been a barrier to some alpine and subalpine species that have their southern limit at the southern end of the Paparoa Range (e.g. *Aciphylla hookeri* and *Dracophyllum townsonii*).

McGlone (1985) accepted that a tectonic hypothesis was credible for the disjunctions of many vascular plant species between Nelson and Otago-Southland whereas glacial extinction in the central Southern Alps had been previously used to explain this pattern. Heads (1998) gave distribution maps for many plant species to illustrate this. The distribution pattern shown is one where a species is present in Nelson and or Marlborough on the Australian plate, and in Otago or Southland on the Pacific plate. The timing of the movement along the alpine fault is such that the Nelson and Otago-Southland ultramafic belt was continuous 25 My ago at the start of the Miocene. By the late Miocene, 10 Ma, the Nelson ultramafic belt was opposite Mt Cook, and by the mid-Pliocene 5 Ma at about the head of the Hope River (Heads 1998). Any disjunction between Nelson and Otago must involve taxa about 25–15 My old, from the early to mid-Miocene. This is too early for alpine plant genera whose habitat was not present before the uplift of the Southern Alps starting about 5 Ma and the cooling of the climate in New Zealand 2 Ma (Fleming 1979). More detailed examination of examples is needed before Heads' and McGlone's hypothesis can be accepted.

Four other reasons can be given for the distribution pattern that Heads believes is caused by tectonic offset. Firstly, that by chance alone, some distributions that fit the tectonic hypothesis will be likely, and statistical proof is needed that this distribution is more common than others. Secondly, distributional information may be incomplete and more complete knowledge of distribution may change the picture. This is the case in *Pleurophascum grandiglōbum* (Heads 1998, p. 169) where a distribution was derived from Sainsbury (1955). The disjunction that was apparent then between Nelson and

South Westland is an artifact of few collections. Thirdly, interpretations of relationships may be incorrect. For example, Dawson (1980) believed that *Aciphylla stannensis* of Stewart Island and *A. trifoliolata* of the Lyell Range, Buller, were sibling species and this was used as an example of a tectonic disjunction by Heads (1998). Dawson's (1980) interpretation of a sibling-species relationship of these two species is probably incorrect, and they are likely to have speciated separately from the widespread species *A. crenulata*. Finally, Heads' limits on what constitutes a distribution that conforms to a disjunction caused by plate shift is very wide, as in this *Aciphylla* example.

Heenan (1996) showed that the Awatere fault separates *Notospartium carmichaeliae* and *Notospartium glabrescens*. Heenan also mentioned a difference of substrate between the two species: *N. carmichaeliae* occurs on greywacke while *N. glabrescens* occurs on Tertiary sedimentary rocks, but considered the fault to be the reason for the disjunction.

Ecological factors influencing biogeography and evolution

More important than geographic barriers are environmental gradients and discontinuities. One of the strongest environmental gradients in New Zealand is the west-east rainfall gradient that is especially pronounced in the mid- Southern alps where the strong topography intensifies the effect. There are many eastern South Island species that do not cross the divide in the central Southern Alps (e.g., *Discaria tomatou*, *Corokia cotoneaster*, *Hebe traversii*, *Helichrysum lanceolatum*, and *Brachyglottis cassinioides*), while *Gaultheria rupestris*, *Lepidothamnus intermedius*, and *Lagarostrobos colensoi* are confined to the western side of the divide (Wilson 1991) and a few east-west species pairs of species may have speciated along this axis, particularly *Celmisia walkeri* and *C. angustifolia*, and *Poa colensoi* and *P. hesperia*.

Flora special to rock types

Uncommon parent materials of soils and the types of soils they give rise to are the second most important factor that has induced speciation in New Zealand *Gentianella*, being the probable cause of c. 12 speciation events (see Discussion and conclusions, Modes of speciation in New Zealand *Gentianella*). I review here the history of views on the importance of different rock types and soils in the New Zealand flora which has changed markedly in the last 20 years, and the comparative importance of the various parent materials that have given rise to species as indicated by the number of species recognised as confined to those rock and soil types.

Some distinctive habitats in the mountains of New Zealand, particularly screes, were

identified by Cockayne (1928) and described by other authors in detail during the 1940s to 1960s (e.g., Fisher 1952). Rock types and the soils derived from them were not until recently considered an important determining factor in the New Zealand alpine flora, for instance by Mark & Adams (1973) who made the following comment:

"Greywacke is particularly prone to frost shattering and is eroding rapidly, resulting in the development of talus slopes or screes, whereas schist is relatively stable. Granite weathers very slowly into a sparse, sandy soil. Apart from this and the striking effect of the ultrabasic rocks in the mineral belt of Nelson-Marlborough and north-western Otago, the different materials seem to have little effect on the distribution of alpine plants." (p. 9)

Druce (1975) disagreed with this summary of the importance of rock types on the distribution of the alpine plants. In the last 15 years, floras distinctive to calcareous and ultramafic rock and associated soils have been identified, initially in accounts of the vegetation of these areas, and more recently, in taxonomic papers.

Soft siltstones with a varying but only moderate amount of calcium carbonate, known in New Zealand as "papa" are extensive in the lower half of the North Island (see Bayly et al., 2000, fig. 17C) and have several species confined to them: *Anaphalioides subrigida* (Glenny 1998), *Hebe stenophylla* (Bayly et al., 2000), and *Sophora godleyi* (Heenan et al., 2001).

Burrows (1964, p. 131) stated that "There is, in New Zealand, no well developed calcicolous vegetation. Only a few species are obligate or near obligate calcicoles. One reason for this may be the comparatively recent emergence of extensive limestone habitats (Pliocene – Pleistocene)." While this may be true of the vegetation communities, recent authors have differed with Burrows as to the abundance of species that are calcicoles.

Druce et al. (1987) studied the soils and vegetation of the western Nelson mountains, including Tertiary limestones of the Matiri area, and listed 11 strong and 21 weak calcicoles in the area. Of the 11 strong calcicoles, five were named species (*Gentiana* [*Gentianella*] *filipes*, *Poa sudicola*, *Senecio glaucophyllus* ssp. *glaucophyllus*, *Colobanthus squarrosus*, and *Epilobium vernicosum*) and the remainder were unnamed taxa. Some have subsequently been named (e.g., *Carex impexa* — Ford 1998).

Druce & Williams (1989) listed 15 strong calcicoles and 13 weak calcicoles on Marlborough limestone areas of the Benmore and Chalk ranges. Of the strong calcicoles, six were named species or subspecies: *Carmichaelia astonii*, *Gentiana* [*Gentianella*] *astonii*, *Myosotis arnoldii*, *Myosotis colensoi*, *Poa acicularifolia* ssp. *acicularifolia*, and *Wahlenbergia matthewsii*.

Williams & Courtney (1998) listed 26 strong calcicoles in Nelson, and 14 weak calcicoles. Of the strong calcicoles, only 10 of the 26 were named species or subspecies. The unnamed calcicoles listed by these authors indicate a belief that the calcicolous flora in New Zealand is still underestimated.

There has been a trend in the last 10 years for New Zealand taxonomists to describe new species confined to limestone and soils derived from ultramafic rock. This may be due to closer attention to areas with these rock types, and perhaps a change in the species concept in use by authors of these species from the "species aggregate" concept to a narrower biological and ecological one.

Poa acicularifolia is a limestone species of Marlborough and Canterbury. A second subspecies, ssp. *ophitalis*, was recently described from Nelson ultramafic soils (Edgar 1986). Heenan & de Lange (1997) described *Carex ophiolithica* from ultramafic soils at Surville Cliffs. Molloy et al. (1999) described *Poa spania* and *Ischnocarpus exilis* from a single limestone outcrop at Awamokoho in Otago. Edgar & Connor (1999) described *Dichelachne lautumia*, a grass restricted to a limestone quarry near the mouth of the Flaxbourne River. Connor & Molloy (1993) and Molloy (1994) described *Australopyrum calcis*, a species found on limestone outcrops in the Leatham Valley in Marlborough, Mt Cass in North Canterbury and Flock Hill. Heenan (1998) reinstated *Sophora longicarinata*, a tree species confined to limestone in Marlborough.

Fewer vascular species have been recognised as confined to the Ordovician marbles of eastern Nelson (Mt Arthur and Mt Owen). Bell (1973) described the vegetation and flora of the Marino Mountains and Lookout Range, and listed species confined to marble on the Marino Mountains but this list contains many species that can be regarded only as weak calcicoles such as *Coprosma propinqua*. Bell analysed the soils of the Mt Owen area and found the cation exchange capacity and calcium ion concentration varied considerably in the soils overlying marble, depending on factors like the depth of the soil overlying the bedrock. Where the peat soil was deep, there was little influence of the calcareous substrate on the soil. *Clematis marmoria* was described from marble on Hoary Head and Crusader in Nelson (Sneddon 1975). *Poa xenica* was recently described from screes below marble bluffs in the Riwaka River area of Nelson (Edgar & Connor 1999). Bayly et al. (2001) described *Hebe calcicola* from the Peel, Lockett, Douglas and Arthur ranges and said that "All known populations occur on outcroppings of marble rocks of the Mount Arthur group, and given the geological complexity of the region ... the substrate specificity of the species is striking". Venter (2002) described a species of *Dracophyllum* confined to marble in Nelson, *D. marmoricola*.

Ultramafic rocks outcrop in New Zealand in three main places: Surville Cliffs at the northern tip of the North Island, in the Nelson area extending to D'Urville Island, and in South West Otago and Southland from the Red Hills to Mavora Lakes area. Some small lenses occur in the central Southern Alps. No species or varieties have been described from the Otago-Southland ultramafic area. A candidate *Gentianella* taxon similar to *G. serotina* is found at West Dome in Southland. However, a number have been described from the Nelson ultramafic area: *Leptinella pyrethrifolia* var. *linariifolia* was recognised by Lloyd (1972) on the basis of a single character — its simple leaf. Edgar (1986) described *Poa acicularifolia* subsp. *ophialitis*. Connor described *Chionochloa defracta* of the Red Hills and Cobb Valley (1988), and *Festuca ultramafica* of Dun Mountain and Mt Duppa (1998). Recently, Venter (2002) described *D. ophioliticum* from ultramafics in the Cobb area. Surville Cliffs has an ultramafic flora of species which differ to varying degrees from their non-ultramafic relatives. Some of these have been named e.g., *Pittosporum ellipticum* subsp. *serpentinum* (de Lange 1998). Edgar and Druce (in Edgar 1998) described an ultramafic species, *Trisetum serpentinum*, with a disjunction distribution, Surville Cliffs and the ultramafic areas of Nelson (Red Hills and Cobb Valley).

The largest area of exposed volcanic rock is in the Central North Island, with two distinctive habitats: ignimbrite cliffs, particularly in river gorges, and loose scoria on the volcanic cones, a particularly difficult substrate for plants because of the temperatures it reaches in summer, and because of its instability. Despite these two distinctive habitats, there appear to be no vascular species specific to volcanic rock in New Zealand. This is in contrast to Hawaii where a number of genera have specialised in this habitat, for instance the silverswords (*Argyroxiphium*), and *Dubautia* (Carlquist 1965).

Schist is the most widespread rock type in Otago and Westland. The elemental composition of the rock is the same as that of greywacke but compression has given it a platy texture. Rock tors and an abundance of silt result from the erosion of schist in Otago and have created some distinctive landscapes and bluff habitats. Central Otago has a number of endemic vascular species, but species that owe their existence to this rock type have not been identified with the exception of Edgar & Connor (1999) who described *Poa schistacea* from schist-derived scree.

Granite makes up part of the ranges of west Nelson (Lead Hills, Glasgow Range to Herbert Range). Large granite domes occur in Westland (e.g., Mt Tuhua and the Hohonu Range) and Fiordland is mostly composed of granite. Williams (1991) mentioned *Gentiana vernicosa* and *G. "Paparoa"* as commonly present on the granite ranges of west

Nelson, but did not specify whether there were any endemics to this rock type. Bell (1973) recorded the flora of the granitic Lookout Range, including an unnamed gentian since referred to as *Gentiana* "Lookout".

At lower altitudes in Westland and western Nelson, weathered granite and granite-derived sandstone on plateaux and outwash terraces has produced especially infertile gleyed and podsolized soils, in some cases so weathered that they consist mainly of quartz sand. At Denniston and Stockton plateaux near Westport, and the Sewell Peak – Mt Davy area near Greymouth there are extensive areas of rock outcrops and poor granite-derived soils. Denniston plateau and Sewell Peak are type localities of *G. montana* ssp. *stolonifera* and *Gentiana townsonii* respectively. *Chionochloa juncea*, a close relative of *C. rubra*, is confined to such soils at Denniston and Stockton. A related habitat occurs on the terraces of outwash and old beach surfaces in Westland, particularly in the Grey and Buller Valleys. These terraces vary in their soil fertility and drainage with age, and this is generally correlated with altitude, the highest terraces having the most nutrient-poor and poorly draining soils. Pakihi is the name used in New Zealand to describe a fern-rushland of *Gleichenia*, *Empodisma*, and *Baumea*, with *Leptospermum scoparium* invading to form scrub. This became a widespread vegetation type on these infertile terraces in North Westland when rimu forest on the terraces was cut or burned during the 19th and 20th centuries (Williams et al. 1987). The flora of these pakihis, as such a recent origin suggests, lacks an endemic element, being a mixture of higher elevation species (e.g., *Epacris pauciflora*, *Carpha alpina*, and *Gleichenia dicarpa*), forest and forest margin species (e.g., *Gahnia* species), oligotrophic mire species (e.g., *Empodisma minus*) and some recent arrivals from Australia such as *Calochilus paludosus*. *Gentianella townsonii* / *G. montana* ssp. *stolonifera* is found on these pakihis. In South Westland, pakihis have formed on similar landforms as in North Westland but are considered to be natural (Mark & Smith 1975), although only as old as the end of the last glaciation (14 000 years b.p.) when outwash terraces were colonised by vegetation. The pakahi vegetation in South Westland appears to have resulted from a combination of inundation of the soils where there is impeded drainage (e.g., lakes formed behind sand dunes) and soils that have become very infertile having developed rapidly under a high rainfall. The only distinct entity of these South Westland pakihis that has been noted is a grass. Connor (1991) observed that at Lake Gault and Skiffington Swamp there was a variant of *Chionochloa rubra* subsp. *occulta* with leaf sheaths that do not fracture, but he did not give this variant taxonomic recognition. The same South Westland pakihis have the candidate taxon *Gentianella* "Gault".

The New Zealand alpine flora

Alpine habitats are challenging environments for plants. Some effects that correlate strongly with altitude impose strong limitations on plant growth. Snow cover limits the growing season for alpine plants in the high alpine zone. Temperatures are lower in the alpine zone, but can become high on bare rock surfaces in mid-summer. Soil development is slower due to reduced chemical weathering and slow organic matter breakdown. Plants of the alpine zone need to survive in skeletal soils with low organic matter and coarse particle size, and in some cases be adapted to penetrating rock with their roots, or to inundated infertile peat soils.

Raven & Raven (1978) characterise the New Zealand mountains as having a highly varied set of habitats that accounts for the radiation seen in *Epilobium*. This applies to other herbaceous and semi-woody plant groups which have undergone rapid and recent radiation in the alpine and subalpine zone, judging by the the number of alpine species in genera such as *Celmisia*, *Hebe*, *Aciphylla*, *Ranunculus*, *Chionochoa*, *Gentianella*, *Raoulia*, *Euphrasia*, and *Myosotis*.

A distinctive habitat in the eastern South Island mountains are the mobile screes created by the shattered of Mesozoic siltstones, mudstones and sandstones that make up large parts of the South Island mountains. Cockayne (1928) listed 28 species adapted to this habitat. Fisher (1952) studied eight Canterbury scree specialists: *Lignocarpa carnosula*, *Lignocarpa diversifolia*, *Leptinella atrata*, *Senecio glaucophyllus* subsp. *discoideus*, *Lobelia roughii*, *Epilobium pycnostachyum*, *Notothlaspi rosulatum*, *Ranunculus haastii*, and *Stellaria roughii*. Fisher found that all of these are succulent, glabrous, are rosette or cushion-forming, and have strong root development that appears out of proportion to their size above ground. All have either small leaves or leaves dissected into small sections. Six of them have reddish pigments in superficial cells. Four have a glaucous bloom. Seven are summer-green perennials, and *Notothlaspi* is biennial (Fisher 1952). A particular kind of scree formed from black carbonaceous mudstones is found in small scattered areas in the South Island mountains. Confined to these fine screes in Marlborough and Canterbury are *Epilobium forbesii* (Raven & Raven 1976; Glenny 1989) and *Rachelia glaria* (Ward et al. 1997).

A habitat that is related to that of screes is that of the fellfields or feldmark that are present on flat or gently sloping ridges and spurs in the drier mountains. Frost-heave on these sites when they are snow-free means plants need to be deeply rooted. In summer the plants are abraded by airborne sand. In winter the plants are protected by snow except on sharp ridge edges where snow is blown clear by wind. Fellfield plants tend to have a

cushion form to minimise exposure to wind and abrasion. More sheltered situations are found around rock outcrops and here a mixture of cushion plants and herbs or semi-woody plants of normal form are found. Fellfields and alpine rock outcrops have a distinctive flora that is most diverse in Marlborough, Canterbury and Otago. Some species characteristic of this habitat are *Aciphylla dobsonii*, *A. simplex*, *A. leighii*, *Anisotome flexuosa*, *Agrostis subulata*, *Carex pyrenaica*, *Celmisia laricifolia*, *Cheesemanianthus enysii*, *Chionohebe pulvinaris*, *C. myosotoides*, *C. ciliolata*, *Colobanthus buehnerianus*, *Parahebe cheesemanii*, *Gentianella divisa*, *Gingidia enysii*, *Haastia pulvinaris*, *H. sinclairii*, *Hebe epacridea*, *H. haastii*, *Hectorella caespitosa*, *Leptinella goyenii*, *Leucogenes grandiceps*, *Luzula colensoi*, *L. pumila*, *Myosotis pulvinaris*, *M. suavis*, *Phyllachne colensoi*, *Poa novae-zelandiae*, *P. exigua*, *Pratia macrodon*, *Ranunculus sericophyllus*, *Raoulia eximia*, *R. grandiflora*, *R. youngii*, and *Rytidosperma setifolium*.

The most favourable habitats in the alpine zone are around streams and flushes because of water and nutrient concentration. Flushes are wetlands at the top of catchments, where water flows through the soil and vegetation but not in an open stream course. They may be permanent or result from snow-melt and temporary. Species adapted to flushes are *Epilobium macropus*, *E. pernitens*, *Ranunculus macropus*, *Poa kirkii*, *Montia fontana*, *Schoenus pauciflorus*, *Juncus novae-zelandiae*, *Bulbinella angustifolia* and *B. hookeri*, *Psychrophila novae-zelandiae* and *P. obtusa*, *Anaphalioides bellidioides*, *Colobanthus apetalus*, *Acaena fissistipula*, and *Isolepis aucklandica*. On low-angled slopes or flat areas, wet areas of lower soil fertility, and tarn margins, this flush vegetation changes to cushionfield dominated by *Oreobolus pectinatus*, *Donatia novae-zelandiae*, *Sphagnum cristatum*, *Carpha alpina*, *Drosera arcturi*, and *Pentachondra pumila* (Wilson 1976).

The origin within New Zealand of alpine plant groups

Too little detail is available on the history of glaciation and mountain uplift for the entire Pleistocene period to allow for any reconstruction of the habitats available for alpine plants throughout this time. No genera in the New Zealand flora have been analysed for a match between phylogeny and distribution yet the materials appear to exist for this in large genera such as *Epilobium*, *Celmisia*, and *Aciphylla*. McGlone (1985, p. 746) considered that "It is apparent that there is a long way to go before the New Zealand biota is known well enough to give great confidence in the deciphering of our internal biogeography ..." and that sound taxonomy and thorough distributional data were required

for the task.

The age-area hypothesis

A method of deriving the place of origin of a geologically recent genus in New Zealand was described by Willis. In 1922 Willis published *Age and Area*, a full statement of a hypothesis that Willis had developed while working on the Ceylon flora. His hypothesis was that the area occupied by a species depends mainly on the age of the species. Willis believed that range expansion rather than by long distance dispersal accounted for the distributions of plants: "Open seas, for example, and even comparatively narrow arms of the sea, like the English Channel, may offer practically insuperable barriers to migration, only to be occasionally passed by a few species, unless with the assistance of man" (Willis 1922, p. 36). His evidence for this in *Age and Area* came mainly from areas of high species endemism such as Hawaii and New Zealand. The pattern he saw in an isolated island group like New Zealand was that speciose genera (e.g., *Ranunculus*) are non-endemic, recently evolved, and abundant, while old genera (e.g., in the conifers) are endemic, widespread but not abundant, having been outcompeted by more recent and successful genera. He claimed also that the distributions of species in a genus in a country like New Zealand were concentric, showing a pattern he described as "wheels within wheels", illustrated in his distribution maps of *Haastia* and *Gunnera* (Willis 1922, pp. 154 and 158). Willis believed that this pattern resulted from evolution of new species from existing more widely distributed ones, so that the smaller "wheels" always lie within the larger "wheels". Willis' theory predated the discussion (e.g., Grant 1971) that concluded that speciation almost always involves geographic barriers, with the resulting species being allopatric.

Willis claimed, in the New Zealand context, that the flora of the outlying islands must be as old as the mainland flora as it must have reached the islands before they were separated from mainland New Zealand by encroaching seas. He saw the Chatham Islands being the best example of this. He claimed that an analysis of the outlying islands floras did indeed show their floras to be old, a claim not supported by recent studies.

Gleason (1924) criticised Willis' hypothesis on the grounds that Willis could only maintain the hypothesis by excluding numerous exceptions and that it became a circular hypothesis: "in other words, the area of a species depends on its age when it does depend on it, and cases in which it does not must not be mentioned." (Gleason 1924, p. 542).

Two examples of exceptions that were mentioned by Gleason were firstly, that movement

of species distributional boundaries back and forth in response to a change in climate has often occurred in North America. Secondly, that isolated species may be unable to move from their current distribution because of their being surrounded by unfavourable habitat, for instance, species on mountain tops. Despite this, Gleason considered that:

"Notwithstanding these peculiarities in its statement, Age and Area is an exceedingly important idea. It is one of the few great general statements in phytogeography. ... It offers to the systematist a means, whether right or wrong, of determining the rank and relationship of species just at a time when such matters are coming prominently to the fore, and may add in the miraculous resuscitation of the dry bones of modern taxonomy. ... it offers a possible means of determining the ancestry of species, and even of genera and families, and enables them to confirm their conclusions by a new body of evidence. And more important than these services, it is calling to the attention of all botanists the facts that the fundamental problem of pure botany today is phylogeny, that phylogeny is intimately connected with taxonomy and distribution, and that the problems of phylogeny offer an exceedingly important and comparatively unworked field for botanical research."
(Gleason 1924, p. 542).

Since 1922 response to Willis' hypothesis has been mainly negative and the hypothesis has been largely forgotten. However, it may be useful in some restricted contexts. It may have application on island groups where it can be established that a genus arrived in New Zealand once and spread from a single point. The New Zealand alpine flora is amenable to such an analysis as it is made up of such neoendemics.

Flower colour in the New Zealand flora

It has been commonly observed (Hooker 1855, Cockayne 1928, Weevers 1952, Godley 1979, Lloyd 1985) that the New Zealand herbaceous flora is lacking in flower colour, a white corolla being the commonest type. In some genera, the more coloured flowers belong to species that are evidently recent arrivals in New Zealand, e.g., in *Epilobium* where the species with coloured flowers tend to be species that are shared with Australia such as *Epilobium billardieranum*. This phenomenon is explained, along with other trends such as simple flower structure and small flowers, by the lack of specialised pollinators in New Zealand, particularly long-tongued bees with colour vision. Despite this, guide marks in the corolla that direct pollinators to nectar rewards occur in

Carmichaelia, *Gentianella*, *Parahebe* and some orchids (Lloyd 1985).

The exception to this trend of lack of flower colour is on the Subantarctic Islands and Chatham Islands where the flowers of ten genera are more coloured than their mainland relatives. These genera are: *Epilobium*, *Anisotome*, *Myosotidium*, *Gentianella*, *Olearia*, *Damnamenia*, *Cardamine*, *Bulbinella*, and *Hebe* (Lloyd 1985). A pollinator explanation of this phenomenon seems unlikely as the Subantarctic Islands and Chatham Islands are even lower in numbers and specialisation than on the main islands of New Zealand, with a complete absence of bees, butterflies or tachinid flies, while the number of species of other pollinating groups present are only 10% of New Zealand mainland numbers (Lloyd 1985). Wardle (1978) suggested that the coloured flowers of Subantarctic Island and Chatham Island species are due to the presence of pigment in flowers being a primitive but non-functional state in the Subantarctic situation, and that mainland New Zealand species were derived from these Subantarctic species and had lost the colour. Lloyd (1985) favoured a functional explanation, as he considered it unlikely that a non-functional characteristic would appear *de novo* in so many unrelated genera, but the only function he could suggest was that coloured flowers become warmer, presumably to the benefit of the ovary's development.

Swenson & Bremer (1997b) tested Wardle's (1968) hypothesis that Subantarctic species with coloured flowers are primitive in *Abrotanella* by looking at the position of species with coloured flowers in their phylogeny. They found that purple central florets in the capitulum were in each case a recent development, occurring independently four times in South America and twice in the New Zealand Subantarctic Islands. In *A. subemarginata* of the Falkland Islands and the New Zealand Subantarctic species *A. rosulata*, flower colour is polymorphic. The primitive state in the genus was yellowish-pale green, and the New Zealand clade was uniformly white except for the two Subantarctic species. This change from yellow-green to white occurred at the time of arrival of the ancestor of the New Zealand species. Swenson & Bremer (1997b) suggested the function of the purple pigment might be protection against intense sunlight.

Not only is red, blue, or purple pigmentation in the corolla common in the Subantarctic Islands and Chatham Islands, but polymorphism for flower colour also seems to be common. Godley (1982) notes it in *Gentianella cerina*, *G. concinna*, *G. antipoda*, *G. antarctica*, and *G. chathamensis*. *Myosotis hortensis* has a "rare white form" noted by Cockayne (Godley 1982). *Damnamenia viscosa* on Campbell and Auckland Islands shows polymorphism in both the disk florets and ray florets (a purple disk and white ray

state is prevalent, a yellow disk and white ray state is occasional, as is a purple disk and pale purple ray state — Godley 1982). *Anisotome antipoda* and *A. latifolia* have flowers that are usually red, but occasionally white (Godley 1982). *Abrotanella rosulata* of Auckland and Campbell Islands is white or yellow-green (Swensen and Bremer 1997b). Polymorphism in *Epilobium confertifolium* (reported in Godley 1982) is doubtful as Raven & Raven (1976, p. 185) point out that natural hybrids with white flowered species occur giving rise to intermediate flower colours in the hybrids.

Polymorphism in corolla colour is not uncommon, but has rarely received adequate explanation. Mogford (1974a and b) found in *Cirsium palustre* that white forms were commoner in coastal cliff situations and at higher altitude. He supposed that their frequency was explained by lower pollinator numbers in these situations where some climatic factor such as rainfall or fog played a part, but failed to prove his explanation. Frias et al. (1975) found a colour polymorphism in *Escholtzia californica* in populations in Chile where it was introduced from California several times from 1895 onwards. They found that corolla colour was related to climate, but in the opposite manner to that observed in California, and concluded that the locus for flower colour is linked by proximity to other genes that are adaptive to different climates.

Jones & Reithel (2001) observed that in experimental populations of *Antirrhinum majus* bumble-bees visited a colour morph preferentially on a particular day, presumably because bumble-bees searched for flowers using a search image of a particular flower morph. This resulted in assortative mating with respect to flower colour. This maintained polymorphism in flower colour.

A study at Duke University on the floral biology of *Ipomoea purpurea* investigated in detail how corolla colour polymorphism was maintained. It was found that four independent genes were responsible for colour control. One controlled production of blue versus pink anthocyanins, a second controlled the distribution of the two pigments on the corolla, a third controlled the intensity of the pigment, and a fourth was an albino gene which controlled whether colour was expressed at all (Epperson & Clegg 1988). Brown & Clegg (1984) found that pollinators preferred dark coloured flowers and that plants of dark and intermediate colour were strong outcrossers. White morphs were visited less by pollinators but often selfed. White morphs displayed frequency-dependent breeding success, a phenomenon they called the "Fisher effect". That is, when white morphs were a low proportion of the population (c. 20%), they were more successful than when they were present at a higher proportion (50% or more). This was due to the combined effects

of a higher efficiency in seed production when self pollinated, very little inbreeding depression, and no pollen discounting. (Pollen discounting is a reduction in the contribution to the outcrossing gene-pool by plants that are mostly selfing). Mojonier & Rauscher (1997) attempted to find a corresponding frequency-dependent success in the coloured morphs, investigating the observation that the heterozygous partly coloured flower morphs produced larger seeds, but they were unable to show that this influenced germination or seedling success. Nevertheless, the Duke University group have at least explained for *Ipomoea purpurea* how frequency-dependent breeding success resulting from both a selfing – outcrossing contrast can create a flower colour polymorphism. It is an explanation that is possibly relevant to the New Zealand Subantarctic Island gentian flora since selfing and flower colour polymorphism are both features of the four species there (Godley 1982).

Part B: A summary of previous work on the genus *Gentianella* and related genera

The genus *Gentianella*

The genus *Gentianella* was described by Moensch in 1794 for *Gentianella tetrandra*, a species described previously under *Gentiana* (as *Gentianella campestris*). The name *Gentianella* was overlooked by Grisebach (1845) in the first synoptic work on the Gentianaceae. Grisebach recognised a number of sections within *Gentiana* such as section *Andicola* and section *Antarctophila*. Kusnezov (1896) was the first to recognise Moensch's name *Gentianella*, but as a subgenus of *Gentiana*. He included in the subgenus all gentian species with nectaries on the corolla rather than the ovary base. Kusnezov wrote the account of *Gentiana* for *Die natürlichen Pflanzenfamilien* (Engler & Prantl 1895) and his classification at subgenus and sectional level was followed by most other authors until the 1950s. He distinguished nine sections within subgenus *Gentianella*: sections *Dasystephana* Griseb., *Andicola* Griseb., *Imaicola* Griseb., *Stylophora* Clarke, *Megacodon* Hemsl., *Amarella* Griseb., *Antarctophila* Griseb., *Arctophila* Griseb., and *Crossopetalum* Froel. These sections were all composed of Northern Hemisphere species with the exception of sections *Dasystephana* (composed of a single South American species), *Andicola* and *Antarctophila*. Section *Amarella* had two South American species assigned to it, *G. ruizii* and one other, not specified.

Section *Andicola* contained more than 50 species, mostly in South America. It also contained the Tasmanian species *G. diemensis* and the New Zealand species *G. saxosa*. The section was defined by Kusnezov (1895, p. 85) as perennial, the corolla wheel- or dish-shaped, the lower part of the filament usually hairy as is also the lower part of the corolla tube between the filaments where there is a fringe. Section *Antarctophila* was composed of *G. montana* of New Zealand, *G. pleurogynoides* of Tasmania, and *G. magellanica* and *G. patagonica* of southern South America. Kusnezov (1895, p. 85) defined the section as non-annual, corolla wheel-shaped, without a fringe in the throat. Hooker's species from New Zealand, *G. cerina*, *G. concinna*, *G. bellidifolia*, and *G. grisebachii*, that were published in 1844 (Hooker 1844a, 1844b), may have been unknown to Kusnezov at the time he wrote since he did not assign them to any section.

The earliest survey of the South American species of *Gentiana* was done by Gilg (1916) who followed Kusnezov in using *Gentianella* as a subgenus. A study of the floral anatomy in the family Gentianaceae (Lindsey 1940), noted that in subgenus *Gentianella*, the nectaries are on the corolla wall rather than at the base of the ovaries, and that all other characters studied agree with this division except in the section *Crossopetalum* which was later segregated as the genus

Gentianopsis.

Warburg (in Clapham et al. 1952) adopted the genus *Gentianella* for the European species and commented that the gentians in the Southern Hemisphere such as those in New Zealand and Australia probably also belonged in that genus. Allan (1961, p. 766) mentioned Warburg's belief that the New Zealand gentians belonged in *Gentianella* and mentioned some characteristics held to define the genus, but said "further study of the N. Z. spp. is required before they are definitely assigned to *Gentianella*."

In South America, Fabris (1953) used *Gentiana* in Kusnezov's sense to include subgenus *Gentianella*. However, by 1955, he began to use the genus name *Gentianella* for five new Peruvian species and made new combinations in *Gentianella* for existing species. In 1960 he distinguished *Gentianella* from *Gentiana* by the following differences: nectaries on the base of the corolla rather than on the base of the ovary, interlobal plications absent from the corolla (they are present in *Gentiana*), calyx without an internal membrane (present in *Gentiana*), lobules with 5–9 principal nerves (three in the lobes of *Gentiana*), calcium oxalate absent from the leaves (present in *Gentiana*), and anthers versatile (fixed in *Gentiana*). *Gentianella* was also used at about this time in a revision of the North American gentian flora (Gillett 1957).

The recognition of *Gentianella* as a genus by Fabris (1955) and Gillett (1957) was part of a trend to recognise at genus level what were originally described as sections of *Gentiana*. Other genera segregated from *Gentiana* at about this time were *Megacodon* (Hemsley) Harold Smith (1936); *Gentianopsis* Y.C.Ma (1951) for what had been *Gentiana* section *Crossopetalum*; and *Comastoma* Toyokuni (1961) for what had been section *Comastoma*.

The sections of *Gentianella* used by Kuznezov (1895) continued to be used in the literature, e.g., by Smith (1967), who used *Gentianella* as a genus, and distinguished within it 6 sections: *Crossopetalum*, *Arctophila*, *Amarella*, *Comastoma*, *Antarctophila*, and *Andicola*. Nilsson (1967), in a review of pollen grains in *Gentianella* and related genera discussed in more detail below, found the species of *Gentianella* section *Crossopetalum* were distinctive but found a confusing pattern of relationships in other sections of *Gentianella*.

A New Zealand author, Philipson (1972) considered in detail the placement of the Southern Hemisphere gentians, describing the main floral characters in *Gentiana s. l.* Philipson described six groups in *Gentiana s. l.*, four of which correspond to five of Kuznezov's sections of subgenus *Gentianella*: sections *Crossopetalum*, *Arctophila*, and *Amarella*, plus the southern gentians that fall into Kuznezov's sections *Andicola* and *Antarctophila*. In addition, he discussed *Gentiana s. s.* and separately, *Gentiana lutea* of section *Coelanthæ*, an unusual species in the genus in its lack of plicae between the corolla lobes and its very deeply divided corolla. Philipson did not

examine Kuznezov's section *Imaicola* (now *Gentianopsis*) or section *Stylophora* and section *Megacodon* of subgenus *Gentianella* (now both *Megacodon*), as he considered them to be more distinct than the other six groups he considered and therefore not relevant to the problem of the genus placement of the southern gentians.

The sections *Andicola* and *Antarctophila* of Kusnezov were rejected by Philipson as "artificial and unnecessary". Philipson pointed out that both sections occur in Australasia and South America, and that the single character of the presence or absence of hairs in the lower corolla and filament bases separates species that otherwise have much in common.

Three options were canvassed by Philipson (1972): (1) to keep the genus *Gentiana* broad as in Bentham & Hooker (1873) and Kuznezov (1891) so that it would include *Gentianella* and other segregate genera such as *Crossopetalum*, an option that by 1972 had lost favour; (2) to split the genera finely on the basis of characters such as presence or absence of plicae at the corolla sinuses, the presence or absence of a fringe of filaments on the corolla, the number of nectaries per filament, and the length of the corolla tube, characters that Philipson pointed out involved some homoplasy; or (3) to divide the species into two large genera *Gentiana* and *Gentianella* on the basis of the position of the nectary. Philipson believed that to follow the third course, as done already in South America by Fabris (1955 and 1960) would lose sight of a distinctive group that he called the southern gentians in a diverse Northern Hemisphere genus. He concluded that "it would be premature to propose new combinations under *Gentianella* for all the New Zealand gentians, though this has been done for most species from the southern regions." (p. 421) and that it was preferable to wait for a better classification using anatomical, chemical and cytological evidence that he hoped would define smaller genera.

Webb (1988, p. 720) mentioned that there was evidence that New Zealand species were closer to *Gentianella* rather than *Gentiana* but that the placement of the Southern Hemisphere group was not easily resolved, citing Philipson (1972). Webb concluded: "At present the adoption of *Gentianella* or *Oreophylax* would be premature".

A revision of the Australian gentians was prepared by Adams (1995) for the *Flora of Australia* (Adams 1996). The number of species in the Australian gentian flora increased from two (*Gentiana pleurogynoides* Griseb. and *Gentiana diemensis* Griseb.) to fourteen. Adams discussed the generic relationships of the subtribe Gentianinae. He accepted the division into *Gentiana* and *Gentianella* based on four characters: three vascular bundles per corolla lobe, the position of the nectary on the corolla, the versatility of the anthers, and lack of reticulation of the seed surface. Adams then examined candidates for the genus of the Australasian gentians. He rejected *Oreophylax*, a name he found was not validly published by Endlicher in 1838, although

used by Löve (1983) for the Australasian gentians. He rejected *Gentianella* on the grounds that he believed the type species, *G. campestris*, to be anomalous in having 4-merous flowers, calyx lobes that are very unequal in size with the smaller lobes fused to the internal surfaces of the larger lobes, and the nectaries being minute and without any surrounding ridge of tissue. He believed that Moensch had made the monotypic genus *Gentianella* on the basis of these supposedly unique characteristics, and that these characteristics are of at least equal significance as the characters that separate other genera segregated from *Gentianella* s. l., i.e., *Comastoma* and *Gentianopsis*. It should be noted here that at least the first two of these characteristics that Adams thought unique to *G. campestris* are present in other Northern Hemisphere species: 4-merous flowers are present in the North American species *G. barbellata*, and *G. simplex* (Gillett 1957) and calyx lobes are very unequal in *G. tenella* (Gillett 1957, fig. 9B).

Adams also rejected three South American genera as candidates for the Australasian gentians: *Selatium* G.Don, *Ulostoma* G.Don, and *Pitygentias* Gilg. He rejected *Ulostoma* on the grounds that its type and sole species, *U. filamentosa* G.Don, has a fimbriate corolla tube. *Selatium* he rejected on the grounds that its eight species have long corolla tubes (whereas the Australasian species have a corolla tube shorter than the lobes) and that some species (including *S. thyrsoides*) have non-versatile anthers, and "somewhat unusual foliage and inflorescence". He rejected *Pitygentias*, which was made by Gilg (1916) for two South American species, *P. pinifolia* and *P. thyrsoides*, on the grounds that *P. thyrsoides* was also placed in *Selatium* which he rejected for the reasons given above, and because Fabris (1958) rejected *Pitygentias* on grounds of taxonomic superficiality.

Adams (1995) clearly preferred Philipson's third option as outlined above, that of continuing the trend of segregating genera from *Gentianella*. The reason for this appears to have been a desire for consistency with the already segregated genera such as *Gentianopsis*, and so as not to lose a distinctive group such as the southern gentians in a large diverse genus. Adams felt, as Philipson did, that there was insufficient understanding of the relationships within *Gentianella* s. l. to produce a phylogeny, but whereas Philipson felt it premature to segregate southern gentians from *Gentianella*, Adams was prepared to take this step.

Adams summed up his understanding of the generic relationships in a dichotomous key in which *Gentianella*, *Comastoma*, and *Jaeschkea* form a group characterised by having the corolla tube longer than the lobes, while the four genera *Frasera*, *Swertia*, *Lomatogonium*, *Lomatogoniopsis*, plus the southern gentians, are characterised by having a short corolla tube. The southern gentians are separated from the four short-tubed genera by having nectary glands that are neither foveolate, pulvinate, nor surrounded by scales (illustrated for *Swertia* in Engler &

Prantl 1895, 4(2): 87, fig. 38 H–T), and that are neither small annuals (usually the case in *Lomatogonium* and *Lomatogoniopsis*) nor single-stemmed plants (as in many *Frasera* and *Swertia* species). This group he described as the new genus *Chionogentias*, with a distribution in Australasia, South America (but not including all South American gentians), and possibly Africa. Adams made names in *Chionogentias* for the Australian gentians with the exception of a single Queensland species of *Gentiana* (Adams 1996). He also placed all New Zealand gentians into *Chionogentias*, making combinations in *Chionogentias* for the species of *Gentiana* recognised by Allan (1961). He did not mention any South American or African species that he considered belonged to his new genus.

Phylogeny

In 1995 Adams believed there was insufficient knowledge of the Gentianinae to make a phylogenetic assessment of the subtribe, but in the same year results of an ITS DNA survey of the subtribe were published (Yuan & Küpfer 1995). Yuan & Küpfer sampled species from the genera *Gentiana*, *Comastoma*, *Crawfurdia*, *Frasera*, *Gentianella*, *Gentianopsis*, *Halenia*, *Lomatogonium*, *Megacodon*, *Pterygocalyx*, *Tripterospermum*, and used *Centaureum* to root their trees. The four species of *Gentianella* they sampled were European, including the type species of *Gentianella*, *G. campestris*. They found that *Gentianella* belongs to a clade that includes *Swertia*, *Halenia*, *Frasera*, *Lomatogonium*, *Comastoma* and *Pterygocalyx*, with *Megacodon* at its base. This clade is distinct from a group of genera that contains *Gentiana*, *Crawfurdia*, and *Triptospermum*. Lack of resolution in the ITS sequences meant that relationships within the larger *Gentianella*-related clade described above were unresolved, but the study showed clearly that *Gentianella* and *Gentiana* are distinct, and clarified the position of genera such as *Megacodon*.

Yuan & Küpfer's resulting strict consensus tree cannot be compared with Adam's assessment of relationships in the subtribe Gentianinae, because the genera considered differ. However, *Gentianella campestris* was sampled and belongs in a clade containing the other three European species of *Gentianella* sampled and so did not bear out Adam's (1995) assertion that *Gentianella campestris* did not belong with the rest of *Gentianella*.

In another molecular phylogenetic study, Hagen & Kadereit (2001) used ITS, *matK*, and the *rpl16*-intron to investigate the relationships of *Gentianella* to related genera, and the relationships within *Gentianella*. Their results showed firstly that *Gentianella* is not monophyletic, having four European and Asian species that grouped with *Lomatogonium* and *Comastoma*. Secondly, they showed that with the exclusion of the *Gentianella* species just

mentioned, the species of *Gentianella* sampled (45 species of 244) are a well supported monophyletic group and have as their sibling group some species of *Swertia* (itself not monophyletic, but appearing in three different clades). They also state that this monophyly is unlikely to be broken by the inclusion of more species, as they believe they have sampled all the important morphological groups in *Gentianella* and immediately related genera.

The sequence data of Hagen & Kadereit (2001) using ITS showed that the fimbriate and efimbriate species of *Gentianella* that they sampled were sibling groups. However, in the matK and rpl16-intron analysis, the efimbriate species of *Gentianella* are paraphyletic in that three efimbriate Northern Hemisphere species, *G. aurea*, *G. stoliczkai* of Eurasia and *G. quinquefolia* of North America, are sister to the fimbriate species (the group of mostly Northern Hemisphere species) and remainder of the efimbriate species (the group of mostly Southern Hemisphere species). They believed, but could not prove, that the fimbriate species are monophyletic. The three efimbriate species *G. aurea*, *G. stoliczkai*, and *G. quinquefolia* share with the fimbriate species a corolla tube longer than the corolla lobes (illustrated for *G. quinquefolia* by Wood & Weaver 1982, fig. 3a-k). This is in contrast to most efimbriate species of South America, Australia and New Zealand in which the corolla tube is short, the exceptions being some bird-pollinated species of South America. They also believed, but could not prove that the efimbriate short corolla-tubed species of *Gentianella* (corresponding to Philipson's southern gentians of South America and Australasia) form a monophyletic group.

Their efimbriate short corolla tube-group contains *Gentianella thyrsoides*, an unusual species in its vegetative morphology, but with a floral morphology normal for the group, as well as the bird pollinated species of South America, and some dioicous species of South America. They also concluded that the sections *Antarctophila* and *Andicola* of Grisebach and Kusnezov are both polyphyletic as they are intermingled on their DNA-based phylogenetic trees.

Hagen & Kadereit (2001) assumed that the time of arrival of *Gentianella* in South America was no earlier than the appearance of an alpine zone in the Andes 3 Ma, and no later than fossil *Gentianella* pollen 1.6 Ma. They then calculated that *Gentianella* arrived in Australasia between 2.7 and 1.4 Ma. They calculated a speciation rate of one species per 17 000 years in the South American *Gentianella* species, by dividing the number of species by the time available.

The taxonomic conclusions of Hagen & Kadereit (2001) are, firstly, that a small group of species presently assigned to *Gentianella* will have to be taken out of the genus. Secondly, that it would be a mistake to divide the fimbriate and non-fimbriate species of *Gentianella* into two genera at present. There is a lack of concordance between the three DNA data sets, and homoplasy in flower characters in the *Gentianinae* when these are mapped onto the DNA trees.

A large number of generic names are available for the efimbriate short tube species of *Gentianella*: *Aloitis*, *Dicardiotis* (both names of Rafinesque 1837), *Selatium*, *Ulostoma*, *Glyphospermum*, *Eudoxia* (all names of G. Don 1837), *Pitygentias* Gilg. 1913, *Arctogentia* Löve 1982, *Kurramiana* Omer and Quaiser 1992, and *Chionogentias* Adams 1995. If at some stage the efimbriate gentians are to be made into a genus, the oldest available name is *Aloitis* whose type species is *A. quinqueflora* (if the genus was to include all the efimbriate species of *Gentianella*) or *Selatium* whose lectotype is *S. thyrsoides* (if the genus was to exclude the three long-tubed efimbriate species of *Gentianella* that appear at the base of their matK tree). The New Zealand and Australian gentians belong to this efimbriate group, and their recommendation is that these and the South American efimbriate species be placed in *Gentianella*. I am following their recommendation.

History of the taxonomy of the New Zealand gentians

In 1786 G. Forster named the first Australasian gentians, *Gentiana montana* and *G. saxosa*, from plants collected in Dusky Sound. This publication preceded publication of the name *Gentianella*. Almost six decades later, Hooker (1844a) in the *Flora Antarctica* described two species from the Auckland Islands, *G. cerina* and *G. concinna*, the latter with two varieties, one of which Kirk later named *G. antarctica* Kirk. Hombron and Jacques later (1853) redescribed *Gentiana concinna* as *G. campbellii* from collections made on D'Urville's second expedition.

Gentiana grisebachii and *G. bellidifolia* were described in *Icones Plantarum* (Hooker 1844b) named from specimens sent to Hooker by Bidwill from the central North Island. In the *Flora of New Zealand* (1854) Hooker accepted for the New Zealand flora five species: *G. montana*, *G. concinna*, *G. saxosa*, *G. cerina*, and *G. pleurogynoides*, the latter a Tasmanian species which he believed also occurred in New Zealand. At the time Hooker (1854) also considered that *G. montana* and his own species *G. grisebachii* were one species. Armstrong (1872) described *Gentiana novae-zelandiae* and later (1880) described *Gentiana hookeri* from specimens collected in Canterbury, Otago, and on Stewart Island. In 1864 a radical reclassification was proposed by Mueller (1864). He made *G. montana*, *G. diemensis*, *G. pleurogynoides*, *G. patagonica*, *G. grisebachii*, *G. bellidifolia*, *G. concinna*, and *G. cerina* all synonyms of *G. saxosa*. Bentham in *Flora Australiensis* (1869) listed for the Australian flora only *Gentiana montana*. He treated *G. grisebachii* and *G. pleurogynoides* as synonyms of *G. montana* and made the variety *G. montana* var. *saxosa*.

The first revision of the New Zealand gentians was completed by Kirk (1895) who recognised all the species of Hooker's 1854 account, but describing five new species: *G. lineata*,

G. spenceri, *G. corymbifera*, *G. antipoda*, and *G. antarctica* (for Hooker's *G. concinna* var. *robusta*). He made five varieties within *G. bellidifolia*: var. *patula*, var. *pulchella*, var. *vacillata*, var. *divisa*, and var. *magnifica*. Within *G. pleurogynoides* he made var. *umbellata* and var. *rigida* for what are now regarded as *G. chathamica* and *G. corymbifera* respectively and he described *G. antarctica* var. *imbricata*. Kirk made Hooker's *G. concinna* a forma within *G. cerina*, citing Hooker's approval for this: "Sir Joseph Hooker agrees with me in considering it impossible to separate *G. concinna* specifically." (Kirk 1895, p. 339). Kirk treated Hooker's *G. grisebachii* and Armstrong's *G. novae-zelandiae* as forms of *G. montana*, and reduced Armstrong's *G. hookeri* into synonymy with Forster's *G. saxosa* and pointed out that the name was preoccupied by a South American species already named by Grisebach.

A year later, Cheeseman (1896) described *Gentiana filipes* from a specimen he had collected from Nelson. In 1906 he gave a comprehensive account of the New Zealand gentians in his *Manual of the New Zealand Flora* (1906) naming four new species: *Gentiana chathamica*, *G. gracilifolia*, *G. vernicosa*, and *G. townsonii*, and a new variety *G. montana* var. *stolonifera*. He raised two of Kirk's varieties to species rank: *G. bellidifolia* var. *patula* to *G. patula*, and *G. bellidifolia* var. *divisa* to *G. divisa*. He did not use the name *G. pleurogynoides*. Cheeseman discussed the type of *G. montana* which Hooker had thought was the same species as his *G. grisebachii*. Examination of type material at Kew and the British Museum had established that *G. montana* was not the same as this species. Cheeseman did not follow Kirk in regarding *G. concinna* as a form of *G. cerina*.

Between 1911 and 1917 Petrie published new gentian species in five papers describing novelties from his own collections: *Gentiana flaccida*, *G. matthewsii*, *G. tenuifolia*, *G. astonii*, *G. tereticaulis*, and *G. gibbsii*. In 1915 Cockayne described *Gentiana serotina* from mid-Canterbury. In 1952 Simpson named *Gentiana vericunda* from Fiordland, a species placed into synonymy of *G. lineata* by Allan in 1961. In 1925 Cheeseman published the second edition of his *Manual of the New Zealand Flora*, updating his 1906 account by adding Petrie's and Cockayne's new species but making no other changes than describing a new variety in *G. bellidifolia*, var. *australis*, with Petrie as the author. In 1926 Petrie published two further species, *Gentiana amabilis* from Southland and *G. spedenii* from Fiordland.

Allan (1961) adopted Cheeseman's 1925 account, but made the following changes: *Gentiana flaccida* and *G. vericunda* were reduced to synonyms of *G. lineata*, and *G. spedenii* a synonym of *G. patula*; *G. matthewsii* was recognised as a species distinct from *G. grisebachii*; *G. bellidifolia* var. *magnifica* was transferred to *G. divisa* var. *magnifica*; and Petrie's *G. amabilis* was placed in synonymy of *G. bellidifolia* saying it was part of a polymorphic group in need of

resolution. In 1967 and 1968 Holub made combinations in *Gentianella* for five New Zealand species (*G. bellidifolia*, *G. corymbifera*, *G. montana*, *G. patula*, and *G. saxosa*) as well as many South American species, but without explanation of why he excluded many of the species recognised by Allan (1961).

In recent years several possible unnamed taxa have been recognised in New Zealand by botanists. In a review of "New Zealand Alpine Plants" (Mark & Adams 1973), Druce (1974) mentioned an unnamed gentian found in the Cobb Valley and elsewhere in North West Nelson. Druce, in the course of botanical field trips throughout New Zealand, compiled geographical species lists that are unpublished but list a large number of unnamed taxa in the genus. Thus, over the last three decades, New Zealand botanists became aware that there were likely to be a number of undescribed gentian species present in New Zealand.

The last New Zealand species to be described was an annual species from Otago, *G. lilliputiana* by Webb, who also commented that "Allan's (1961) treatment of *Gentiana* is unsatisfactory. Several undescribed species are now recognised while others accepted by Allan are poorly defined or do not warrant recognition as distinct species." (Webb 1990).

Combinations for most of the New Zealand gentian species in *Gentianella* have been provided by Ho & Liu (1993). They gave no further justification for this other than to point out that *Gentianella* had been segregated from *Gentiana*. The species they made combinations for were those of Allan (1961) with two exceptions: they followed Kirk in making a combination for *Gentianella bellidifolia* var. *divisa*, and recognised *Gentianella spedenii*. Combinations were not made for *Gentiana amabilis*, *G. lineata*, *G. lilliputiana*, or *G. serotina*.

Adams (1995) rejected the use of species names based on New Zealand types for the Australian flora as he considered that none of the Australian taxa were shared with New Zealand. He traced the history of use of the names *G. montana* and *G. saxosa* in the New Zealand and Australian floras. Adams also made combinations in his new genus *Chionogentias* for the New Zealand gentians recognised by Allan (1961). Adams considered that *G. demissa* might be related to *G. cerina* of the Auckland Islands, and that *G. grandis* might be related to New Zealand's *G. corymbifera*. As only the type is known for *G. grandis* and there appear to be no basal rosette leaves on the specimen, this would be difficult to confirm.

Difficulties of distinguishing the New Zealand species from each other were alluded to by Kirk (1895), Cheeseman (1906, 1925) and Allan (1961). Kirk (1895, p. 331) said: "... the New Zealand forms are remarkable for the excessive amount of variation exhibited by several. Not only does it affect the habit, stature, branching, texture, and inflorescence as well as the shape and size of the flowers, but it extends to the reproductive system: both calyx and corolla vary

greatly in the depth to which they are divided, and in the outline of the segments, while even the form and position of the ovary are affected in some instances: the typical form having the ovary sessile, while in a trivial variety it becomes stipitate. This variation renders it difficult to find characters sufficiently stable to warrant the constitution of species and make it necessary to define an unusually large number of varieties. There is evidence leading to the conclusion that hybridisation is largely responsible for this condition, but to a great extent it is due to environment." Kirk goes on to describe how for *Gentiana concinna* – *G. cerina* there is a large coastal rupestral form, and a small bog form, but that "All these forms are connected by a series of insensible gradations, so that it is impossible to say at any given point in the series, 'Here is a line of division'. The change is so gradual that, although it can be easily made out, it is impossible to say where one form begins and another ends."

Cheeseman (1906, p. 446) made similar comments saying: "The species are in all countries highly variable and difficult of discrimination, but nowhere more so than in New Zealand, where they are peculiarly unstable, presenting a bewildering multitude of closely allied forms, to arrange which systematically is a most perplexing task there is really little choice between giving the rank of species to a considerable number of closely allied forms or of reducing the whole of them to two or three comprehensive aggregates. In the latter case it would be necessary to distinguish the forms as varieties, which is practically the same arrangement under a different name. Owing to their extreme variability, the student will find it difficult to identify the species until he has collected a large series of specimens from widely separated localities, and has thus become acquainted with the range and trend of variation."

Cheeseman (1906, 1925) did not provide a key to the species, but listed seven groups with brief diagnoses of each. His arrangement depended heavily on the distinction between annual and perennial species, despite difficulties in establishing this for some species, e.g., for *G. gibbsii* where Cheeseman says: "Said to be annual but the few specimens I have seen might well be perennial." (Cheeseman 1925, p. 726)

Allan (1961, p. 779) cited Cheeseman's comments above and added: "It is probable that most spp. are very plastic and that the exact nature of the habitat plays a large part in producing different forms." He also mentioned that the difficulties of the genus are made worse by the difficulty of cultivating the species. Allan provided a key to the species of the main islands but did not attempt this for the Subantarctic Island and Chatham Island species. Allan (1961, p. 779) comments that "The key provided may be helpful, but will not solve all the student's problems."

The use of infraspecific ranks in *Gentianella*

Overseas taxonomists of *Gentianella* have often used infraspecific ranks because of the geographical variation that seems characteristic in the genus world-wide. The rank of form has often been used in the European species. Usage as indicated in Index Kewensis (1997) is about an equal mixture of subspecies and variety, with no trend toward the use of subspecies rank in recent years. Adams (1995) used the rank of subspecies, in conformity with a decision of the *Flora of Australia* editors to adopt subspecies as the sole infraspecific rank.

In the New Zealand gentians the categories of variety and form are the subspecific ranks that have been used (Table 2). Hooker (1855) listed varieties using only Greek letters, i.e., var. α , var. β , var. γ , etc. with diagnoses of these, and geographical ranges. These are not validly published names, as they were in his *Flora Antarctica* (1844a) where he named within *Gentiana concinna* "var. β *elongata*" and "var. γ *robusta*" with Latin diagnoses and geographic ranges for the two.

Table 2 Infraspecific taxon names applied to the New Zealand gentians, arranged by publishing author.

Gentiana concinna var. *elongata* Hook.f.
Gentiana concinna var. *robusta* Hook.f.
Gentiana antarctica var. *imbricata* Kirk
Gentiana antipoda forma *pallida* Kirk
Gentiana antipoda forma *rubra* Kirk
Gentiana bellidifolia var. *divisa* Kirk
Gentiana bellidifolia var. *magnifica* Kirk
Gentiana bellidifolia var. *patula* Kirk
Gentiana bellidifolia var. *pulchella* Kirk
Gentiana bellidifolia var. *vacillata* Kirk
Gentiana cerina forma *concinna* Kirk
Gentiana cerina forma *suberecta* Kirk
Gentiana montana forma *novae-zelandiae* (J.B.Armstrong) Kirk
Gentiana pleurogynoides var. *rigida* Kirk
Gentiana pleurogynoides var. *umbellata* Kirk
Gentiana saxosa var. *recurvata* Kirk
Gentiana bellidifolia var. *australis* Petrie ex Cheeseman
Gentiana cerina var. *suberecta* (Kirk) Cheeseman
Gentiana grisebachii var. *matthewsii* (Petrie) Cheeseman
Gentiana grisebachii var. *novae-zelandiae* (J.B.Armstrong) Cheeseman
Gentiana montana var. *stolonifera* Cheeseman
Gentiana divisa var. *magnifica* (Kirk) Allan

Kirk used both variety and form frequently, mostly to erect new varieties and forms in the Subantarctic Island gentian flora, and to change the rank of Hooker's varieties and species, both upwards and downwards. Whereas Hooker saw the Campbell Island gentian as a variety of one

of the Auckland Island species (*G. concinna* var. *elongata*) Kirk raised it to species rank as *G. antarctica* noting that Hooker had not seen it in flower and suspected it to be a distinct species. He transferred Hooker's *G. concinna* var. *elongata* to *G. antarctica* var. *imbricata*, but believed it was probably also a distinct species. He enlarged Hooker's concept of *G. cerina* to include Hooker's *G. concinna*, and made a new forma *suberecta*. Within *G. antipoda*, Kirk made two forms, forma *pallida* and forma *rubra* for the striking colour variation that is seen in that species.

In addition, Kirk made five new varieties within *G. bellidifolia* and made Hooker's species *G. grisebachii* and Armstrong's *G. novae-zelandiae* forms of *G. montana* on the grounds that he thought that *G. grisebachii* and *G. montana* grade into each other, and that *G. novae-zelandiae* was a temporary state of *G. montana* that is abundant in moist seasons. He also made two new varieties within *G. pleurogynoides*, var. *umbellata* from the Chatham Islands (now *G. chathamica*) and from ultramafic substrates on D'Urville Island, and var. *rigida* (which is *G. corymbifera*). Kirk believed his varieties were geographic variants in most cases, but that on further consideration they might be considered full species. Kirk explained his use of variety thus:

"In the following descriptions an attempt has been made to differentiate the more striking permanent departures from the typical form of the species as varieties, but the success attained is less complete than could have been wished, although possibly sufficient has been done to prevent that sense of confusion which often troubles the minds of young students on finding a number of apparently dissimilar plants united under a common name." (p. 333).

Infraspecific ranks were used sparingly by Cheeseman (1906) who described a new variety *G. montana* var. *stolonifera* and raised Kirk's *G. montana* forma *novae-zelandiae* to a variety after being told by N. E. Brown at Kew that the types of *G. montana* and *G. novae-zelandiae* in no way resembled each other. He raised Kirk's *G. bellidifolia* var. *divisa* and *G. bellidifolia* var. *patula* to species rank.

In the preface to the *Flora of New Zealand* volume 1, (Allan 1961), Moore stated that Allan recognised only the rank of variety among those allowed by the International Code of Botanical Nomenclature. Allan put most of the existing varietal names in the gentians in small type, a procedure he appears to have used to report names but to make no judgement over their distinctness, or to reinforce a comment made in the text that he thought they were environmental forms, or graded into other forms. Allan appears to have regarded most of Kirk's varieties with some scepticism (e.g., *G. saxosa* var. *recurvata* which he dismissed as falling within the variation of *G. saxosa*). The exceptions to this rule in *Gentiana* were *G. divisa* var. *magnifica* which he transferred from *G. bellidifolia* to *G. divisa*, *G. montana* var. *stolonifera*, and *G. cerina* var.

suberecta. He assigned *G. pleurogynoides* var. *umbellata* to *G. chathamica*.

Allan was more economical in the use of infraspecific ranks than Kirk, and in his own new names and combinations conformed to the usage established earlier by Hooker of using variety. Nevertheless, it is clear from Moore's remarks (in Allan 1961) that he wished to recognise only one infraspecific rank and would have been equally happy to have used the rank of subspecies rather than variety had the Code specified this.

Review of supplementary forms of evidence in studies of *Gentianella* and related genera

In the revision presented here, pollen surface patterns, leaf anatomy and leaf cuticle patterns, seed size and surface patterning, and chromosome counts were investigated in the attempt to supplement the sparse morphological characters available in the New Zealand gentian species. Previous investigations of these kinds of evidence in *Gentianella* are summarised here.

Pollen surface patterns

Nilsson (1967) studied the patterns in the subtribe Gentianinae that includes *Gentiana*, *Gentianella*, *Swertia*, *Crawfordia*, *Halenia*, *Veratrilla*, *Megacodon*, *Tripterosperrum*, *Ixanthus*, *Jaeschkea* and species belonging to two genera that have been segregated from *Gentianella* since 1967, *Gentianopsis* and *Conostomum*. The pollen grains of the Gentianaceae are mostly 3-colporate, occasionally 2- or 4-colporate. Nilsson classified the surface patterns into five groups: striate, striate-reticulate, reticulate, spiniferous, and smooth and within these five groups he distinguished five subdivisions. Lirae, or ridges, form the striate or reticulate pattern and are supported by vertical baculae which may be one or more per ridge. In the case of striate pollen grains, the lirae dominate in SEM photographs and in light microscope views. In striate pollen grains, short bridges between the lirae are at a lower level than the lirae and less conspicuous, while in the case of reticulate pollen grains, these bridges are at the same level as the lirae. Within *Gentianella*, Nilsson adopted the sectional classification of Kusnezov which has been criticised by more recent authors as containing polyphyletic groups (e.g., by Philipson 1972; Hagen & Kadereit 2001). Both striate and reticulate types are present in different sections. For instance, the reticulate type is present in section *Amarella* in *G. wislizenii*, while all other species sampled in the section are striate or striate-reticulate. Similarly, in South American species of section *Andicola*, *G. magellanica* is of the reticulate type while all other species sampled in the section are striate or striate-reticulate. Three New Zealand species were sampled to represent section *Antarctophila*: *G. montana*, *G. patula* and *G. corymbifera*. All three are of the striate type, but the pattern is coarser in *G. montana*. In sectioned pollen grains there are no differences

in the baculae supporting the lirae (that create the striate pattern) among the sections of *Gentianella*. Thus Nilsson's survey, while finding some distinct pollen surface types in genera such as *Crawfordia*, *Tripterospermum*, and what is now *Gentianopsis*, did not find good surface pattern characters in *Gentianella* at sectional level. The lack of an understanding of relationships below sectional level and the small numbers of *Gentianella* species sampled did not allow the survey to uncover any relationships at a lower level.

Chemistry

Carbonnier et al. (1977) analysed xanthonenes from *Gentiana*, *Gentianella*, *Gentianopsis*, and *Comastoma* species and found that many of the 31 different xanthonenes were shared by genera or sections within those genera and that this was sufficient to construct a phylogenetic tree. Two New Zealand species were sampled, *G. bellidifolia* and *G. corymbifera*, but no xanthonenes unique to those two species were found.

Xanthonenes and flavonoids were extracted from *Gentianella corymbifera*, *G. serotina*, and *G. bellidifolia* by Massias et al. (1981) who found 13 compounds. Twelve of these were already known from *Gentianella* species, including swertisin, a compound found in all *Gentianella* species sampled including *G. bellidifolia* and *G. serotina*, *G. campestris*, *G. germanica* and *G. ramosa*. Conversely, none of the xanthonenes found in *Gentiana* were present in *G. corymbifera*. This result supported the separation of *Gentiana* and *Gentianella* and the homogeneity of *Gentianella*. The three New Zealand species sampled did not contain decussatin, a compound found in European *Gentianella*, *Comastoma*, *Crossopetalum*, and many species of *Gentiana*. They concluded from this that European taxa are less advanced than species from New Zealand. These two studies only sampled three Southern Hemisphere *Gentianella* species, all from New Zealand, but indicate that flavonoid and xanthone chemistry might be informative in establishing relationships within Southern Hemisphere *Gentianella*.

Chromosome counts

Gentiana s. s. has a base number of $x = 6$ or 13 (Ho & Liu 1990). Some of the genera that Yuan & Küpfer's (1995) sequencing study showed are closest to *Gentianella*, and which have the nectaries on the corolla wall rather than on the style base, have base numbers as follows: *Swertia*: $x = 9$; *Halenia*: $x = 11$; *Lomatogonium*: $x = 5$; *Comastoma*: $x = 5$; *Gentianopsis*: $x = 11$, while *Gentianella* itself has a base number of $x = 9$ (Ho & Liu 1990). Löve (1953) reported nine counts of $2n = 36$ in *Gentianella s. s.* (excluding what are now *Gentianopsis* and *Comastoma*). Gillett (1957) reported counts of $2n = 36$ for four species (*G. amarella*, *G. campestris*, *G. aurea*,

and *G. quinquefolia*), all of section *Amarella*. European species of *Gentianella* also share $2n = 36$. Few counts have been published of South American species. Moore (1981) reported $2n = 36$ for *Gentianella magellanica* and Pringle (1986) reported $2n = 36$ for three Andean species, *G. cerastioides*, *G. pavonii*, and *G. rapunculoides*. No counts have been published for any of the Australian species.

Three chromosome counts of *Gentianella* species reported in the period 1975–1997 (Goldblatt & Johnson 1975–1997) deviate from this number. Gagnidze et al. (1992) reported $2n = 18$ for *Gentianella umbellata*, a species previously reported as having $2n = 36$ by Farvarger & Huynh (1965). Dalgaard (1989) reported $2n = 18$ for *Gentianella aurea*, which has otherwise been reported as having $2n = 36$ (e.g., by Gillett 1957 and Löve 1953). Dobeš et al. 1997 reported $2n = 18$ for *Gentianella austriaca* which has otherwise been reported as having $2n = 36$ (Löve & Löve 1986).

Numerous counts of New Zealand species have been done by Löve, Hair, Beuzenberg, and Post, and were summarised in Hair et al. (1980), and are reported here in the taxonomy section after each species or subspecies description. The only named taxa that have not been counted are *G. astonii* s. s., *G. divisa* var. *magnifica*, *G. spenceri*, *G. gibbsii*, *G. concinna*, *G. cerina*, and *G. lilliputiana*. All counts of New Zealand species were of $2n = 36$, with the exception of one count of $2n = 18$ from a gentian of unknown identity collected on the Barrier Range, Fiordland. The possibility that the $2n = 18$ population might represent a population least changed from a species ancestral to all others in New Zealand made it important to obtain further counts of fresh specimens from the Barrier Range.

Seed studies

Miège & Wüest (1984) studied the surface of seeds of *Gentiana* and *Gentianella* using SEM photography, sampling 22 European species of *Gentiana* and six European species of *Gentianella*. While in *Gentiana* they found sufficient differences in the reticulate seed surface to construct a key to separate 20 European species on seed characteristics alone, in *Gentianella* they found the seeds to be uniform in having an almost smooth seed surface.

Leaf anatomy and leaf cuticle patterns

No studies of leaf anatomy in *Gentianella* or close relatives appear to have been published. However Klackenberg (1985) examined leaf cuticles in *Exacum* (Gentianaceae), a genus of 64 species of Asia and Africa, and found three types of stomatal subsidiary cell walls: an anomocytic type with zigzagged walls, an anisocytic type with straight walls, and a third type

with thickened straight walls, each type characterising a monophyletic group.

Breeding systems in New Zealand *Gentianella*

A notable feature of *Gentianella* species of New Zealand's outlying islands are their smaller floral parts than their mainland relatives, a phenomenon usually associated with selfing.

Godley (1982) studied the life cycle, pollinators, ovary size, ovule number, seed set, corolla colour, and anther attitude of *G. antipoda* (Antipodes Islands) and *G. antarctica* (Campbell Island) relative to other New Zealand species. Both species have relatively small flowers, low ovule numbers, and small anthers. Most remarkable was the low ovule number in *G. antipoda* with a median number of four ovules per ovary, but with high seed set. Godley supposed that geitonogamy rather than autogamy was responsible for the high seed set in *G. antipoda*, as the extrorse anthers make autogamy difficult.

In contrast, individual flowers of *G. lineata* and *G. gibbsii* of Stewart Island are not protandrous and self-pollinated (Webb & Pearson 1993). Webb & Pearson claimed that *G. chathamica* has a simultaneous male and female phase but that the anther filaments are short so that while the anthers are presented horizontally, they do not cause self-pollination.

Self-compatibility of *G. saxosa* and *G. serotina* in the glasshouse was studied by Webb & Littleton (1987) who found that artificially cross-pollinated and self-pollinated flowers set equal amounts of seed while unpollinated flowers set no seed. They established that for these species at least, there is no self-incompatibility. They found that flowers of these two species close after pollination. For flowers newly in the female phase, they were closed the day following pollination, while those which had been receptive for longer closed more slowly and in some cases not at all. They also found that flowers pollinated soon after the start of the female phase matured a higher proportion of their ovules than those pollinated later.

Life cycle in *Gentianella*

The gentians are the largest genus in the New Zealand flora with a high proportion of monocarpic species. Hooker (1844a, 1855), Kirk (1896), Cheeseman (1906, 1925), Petrie (1911, 1912a, 1912b, 1916, 1917) and Allan (1961) all stated whether each species they recognised was annual or perennial, but none used the term biennial.

Only Cockayne (1915) made a distinction between annual and biennial forms in stating that his species, *G. serotina*, was biennial but with a question mark to this. None of these authors stated how annual species could be distinguished from perennial species. It can be presumed that by "annual", the five authors above (but not Cockayne) meant what would now be termed

monocarpic.

Difficulties in assigning a life cycle type to plants may be contributed to by two factors. Firstly, biennials may be facultative. Kelly (1985) proposed the term "facultative biennial" for the majority of biennials which do not flower invariably in their second year, i.e., they flower once they have amassed sufficient resources to do so, in one year, two years, or more. Secondly, there may be variation within a species, between populations, or within populations. Only by following the progress of individual plants or a population in successive years, can it be determined whether biennials are strict or facultative and this has not been done for any New Zealand monocarpic gentian species and is not investigated here. Table 3 summarises the proportions of monocarpic and polycarpic species in New Zealand with those in some other countries.

Table 3 Numbers of monocarpic (strict annuals; strict and facultative biennials) and polycarpic species in *Gentianella* in New Zealand and some other countries.

	Annual	Biennial	Polycarpic
Europe	0	18	0
China	8	1	0
North America	1	2	1
Ecuador	2	1	19
Argentina	6	4	8
New Zealand	2	10	13
Australia	0	13	3

Sources: Europe: Tutin (1972); China: Ho & Pringle (1995); North America: Gillett (1957); Ecuador: Fabris (1960); Argentina: Fabris (1953); New Zealand: this work; Australia: Adams (1995).

METHODS AND MATERIALS

The classification in Allan (1961) was used as a starting point for the taxa to be examined. In addition, 21 candidate taxa were considered. These were known mainly from tag names (informal, unpublished names) on specimens at CHR, where A. P. Druce had made most of the determinations of specimens. Tag names of A. P. Druce are *Gentiana* "stellar", *G.* "Cobb", *G.* "volcanic plateau", *G.* "Paparoa", *G.* "long narrow leaves", *G.* "Lookout", *G.* "Red Hills peat", *G.* "Rimutaka", *G.* "Skeleton", *G.* "Skippers", *G.* "decumbent", and *G.* "Barefell" (Druce 1992b). In addition, between 1994 and 2000, B. Molloy collected, studied, and grew gentians from limestone outcrops on the east coast of the South Island from Marlborough to Otago. Tag names of these were candidate taxa are *Gentiana* "Brown", *G.* "Ward", *G.* "Manahune", *G.* "Pareora", and *G.* "Awahokomo", the last referred to by Druce (1992b) as *G.* "Waitaki". Two candidate taxa were recognised by P. Wardle in his 1975 list of vascular plants of South Westland with CHR vouchers cited; these are referred to as *G.* "subalpina" (Wardle's *Gentiana* cf. *patula*), and *G.* "Gault" (Wardle's *Gentiana* cf. *spenceri*). A. Wilton collected a gentian on the Chalk Range, Marlborough in 1997 that appeared to be distinct from *G. astonii*; this candidate taxon is referred to as *G.* "Chalk". A specimen of *G. saxosa* in CHR collected by D. Norton and P. de Lange at Charleston, including a photograph of the flower with coloured corolla veins, pointed to the continuing existence of a very isolated population of *G. saxosa* noted by Cheeseman (1925). This candidate taxon is referred to as *G.* "Charleston". All of these candidate taxa were collected in the course of field work.

Herbarium specimens were made by collecting whole plants in the field, including roots. These were kept fresh in plastic bags with damp *Sphagnum* in a chilly-bin and then in the refrigerator until they could be measured. Plants kept in this way lasted up to three weeks. Flowers and leaves were also preserved in FAA and used for leaf anatomy descriptions and to verify some floral measurements. Limited numbers of measurements were taken from herbarium specimens to supplement the measurements made from fresh plants. Pedicel and flowering stem diameter was measured from both fresh and dried material. Flower measurements are from fresh flowers, FAA-preserved flowers, or rehydrated herbarium specimens. There appeared to be no differences in dimensions of flowers from these three sources. In the Taxonomy section, "Specimens examined" lists specimens that were examined fresh or as FAA-preserved specimens and scored for all available characters. Herbarium specimens that were used to supplement measurements are

listed there if they were scored for most characters, particularly if they were used to contribute to a multivariate analysis. "Specimens examined" is not a list of what can be regarded as typical or representing the range of the species. All specimens at AK, CHR, OTA, and WELT were seen. Attempts were made to grow some of the gentian species from seedlings collected in the wild, but losses from these were too great to justify the effort of growing the numbers required for analysis of variation of glasshouse-standardised plants.

Collections often consisted of more than one plant in order to represent the size range at a site. Size extremes were chosen for measurement of macroscopic parts (e.g., rosette leaves), and at least three rosette leaves were measured from each collection. Flower measurements were usually taken from three flowers from each population.

To limit variation due to flower age, flower dimensions were taken from flowers only in male phase, i.e., at the stage between the opening of the anthers that marks the start of the male phase and the opening of the style arms that marks the start of the female phase. All New Zealand *Gentianella* species are protandrous with the noted exceptions of *G. chathamica*, *G. lineata*, and *G. gibbsii* (Webb & Pearson 1993) and the onset of each stage is easily observed. The disadvantage of this restriction on the phase of development of the flower is that dimensions taken from flowers in female phase will often exceed the measurements given.

A character set using presence absence characters, multistate characters, and quantitative characters was devised, and recorded in Delta format (Dallwitz et al. 1993). Seventy one characters were used to characterise each species, of which 35 characters were discrete and 28 continuous, the remainder descriptive or habitat characters. A score sheet was created from the Delta character file. Each specimen, often more than one plant, was scored on copies of this score sheet. The data sheets were used to create and modify the Delta items file.

Table 4. Delta character set.

- | | |
|--|--|
| #1. plants/
1. monocarpic/
2. polycarpic/ | 2. half way up flowering stem/
3. near apex of flowering stem/ |
| #2. <plants life cycle>/
1. annual/
2. biennial/
3. perennial/ | #14. rosette leaves <shape>/
1. linear/
2. narrowly elliptical/
3. elliptical/
4. orbicular/
5. obovate/
6. narrowly obovate/
7. ovate/ |
| #3. height in flower/
<> cm/ | #15. <rosette leaf length>/
<> mm long/ |
| #3. caudex/
1. unbranched/
2. branched/ | #16. <rosette leaf width>/
<> mm wide/ |
| #4. <caudex length>/
cm long/ | #17. <rosette leaf colour>/
1. green/
2. tinted crimson below/
3. tinted purple-black/
4. <other>/ |
| #5. root/
1. branched/
2. unbranched/ | #18. <rosette leaf channelling>/
1. flat/
2. keeled/
3. channelled/ |
| #6. <root diameter>/
mm diameter at stem base/ | #19. <rosette leaves>/
1. not recurved/
2. recurved/ |
| #7. flowering stems/
1. terminal only/
2. terminal and lateral/
3. lateral only/ | #21. petiole <width at base>/
<> mm wide at leaf base/ |
| #8. <lateral flowering stems, number per plant>/
<> per plant/ | #22. flowering stem leaves <description>/ |
| #9. <terminal flowering stem diameter>/
<> mm diameter at base/ | #23. <rosette of leaves>/
1. absent/
2. present but not very distinct from flowering stem leaves/
3. present and distinct from flowering stem leaves/ |
| #10. <flowering stem colour>/
1. green/
2. tinted crimson/
3. tinted purple-black/
4. <other>/ | #24. <number of flowers per plant> with/
<number> flowers/ |
| #11. lateral flowering stems/
1. erect/
2. decumbent/ | #25. pedicels/
1. one per leaf axil/
2. one or two per leaf axil/ |
| #12. flowering stem internodes/
<number> per stem/ | #26. <pedicel length>/ |
| #13. lowest pedicels from/
1. near base of flowering stem/ | |

- <> mm long/
- #27. <pedicel diameter>/
<> mm diameter/
- #29. <flower length>/
<> mm long/
- #30. calyx/ <> mm long/
- #31. calyx lobes/ <length> mm long/
- #32. <calyx lobe colour>/
1. green/
2. green tinted purple-black/
3. <other>/
- #33. <calyx lobes>/
1. plane/
2. recurved/
- #34. <calyx> lobe apices <shape>/
1. acute/
2. obtuse/
- #35. <calyx> lobe margins/
1. smooth/
2. minutely serrulate or papillose/
- #36. hairs at calyx-corolla fusion line/
1. absent/
2. present/
- #37. hairs on inner calyx surface/
1. absent/
2. present/
- #38. corolla <length>/
<> mm long/
- #39. <corolla colour>/
1. white/
2. veins coloured/
3. coloured/
- #40. corolla tube/
<length> mm long/
- #41. corolla lobes/
<length> mm long/
- #42. <corolla lobes>/
<width> mm wide/
- #43. <corolla lobe shape>/
<obovateness>
- #44. hairs at sinus/
1. absent/
2. present/
- #45. nectary/
<> mm from corolla base/
- #46. filaments <length>/
<> mm long from corolla base/
- #47. <filament width>/
<> mm wide/
- #48. anthers <length>/
<> mm long/
- #49. anther wall <colour>/
1. yellow/
2. blue-black/
3. dark red/
4. <other>/
- #50. anther mouth <colour>/
1. yellow/
2. orange-red/
- #51. <anthers position at anthesis>/
1. introrse at anthesis/
2. extrorse at anthesis/
3. horizontal at anthesis/
- #52. pollen/
<> um diameter/
- #53. <pollen>/
1. yellow/
2. black/
3. pale orange/
- #56. stigma <colour>/
1. colourless/
2. crimson/
3. blue/
4. purple/
- #57. ovule number/
- #58. ovary colour after gynoesis/
1. yellow/
2. blue/
3. purple/
- #59. dry capsule <length>/
<> mm long/

- #60. seed <size>/
 <> mm diameter/
- #61. <seed shape>/
 1. spherical/
 2.<other>/
- #62. <seed colour>/
 1. yellow/
 2. brown/
 3. dark brown/
- #62. calyx lobes <width>/
 <width> mm wide at base of lobe/
- #63. habitat <vegetation type>
- #64. <habitat moisture>/
 1. dry/
 2. moist/
- #65. distribution: <Land District>
- #66. based on <collection>/

Eight characters were added part of the way through the study, and, because of the inconvenience of having data sheets with different character numbering, were kept at the end of the data set:

- #67. altitude range/
 <> m a.s.l./
- #68. dry terminal flowering stem <diameter>/
 <> mm diameter/
- #69. dry pedicel <diameter>/
 <> mm diameter/
- #70. stoloniferous shoots arising from branched caudex/
 1. absent/
 2. present/
- #71. calyx sinus hairs/
 1. absent/
 2. sparse/
 3. abundant/
- #72. petiole <distinctness>/
 1. absent/
 2. indistinct/
 3. distinct/

#73. calyx lobes, ratio of width of largest pair to width of apical lobe/

#74. calyx lobe, ratio of width to height/

#75. female flowers <lacking anthers>/

1. absent/

2. rarely present/

3. often present/

#76. stigma length/

<> mm/

Morphological and geographic variation within the species groups was analysed using several methods. The distribution of each species and candidate taxon was mapped using all specimens at AK, CHR, and WELT to establish the geographical relationships between taxa. These maps are presented in the Taxonomy section. Leaf silhouettes were related to locality to show geographical variation. Principal components analyses were performed using the statistical analysis package Systat. Characters chosen for these analyses are mostly the same for each analysis, but in some cases were supplemented with characters like pedicel length that were important in only some species groups. Principal components analyses were performed separately for each group of species to simplify the interpretation of the scatterplots, and because the relationships within the groups was at issue, not those between the groups. For each specimen entered into an analysis, the mean for any character such as leaf length was used where replicates of measurements were available to reduce the scatter due to within-plant and within-population differences. For each analysis, the scores for principal components I and II are presented for each specimen in the analysis. The character scores (eigenvectors) are also presented as these show the contributions of the characters to each component score (eigenvalue). The group analyses give some objective measure of the degree of difference between existing species and between these and the candidate taxa.

The Delta items file was used to compile species descriptions, using Delta's natural language description writing facility. The descriptions were then individually modified to improve the sense. They were also improved later using herbarium material and the addition of mean values from the data sets compiled for the principal components analyses and comparisons of means.

Supplementary sources of evidence

Six other kinds of evidence were gathered to supplement the main evidence of plant morphology. The data from these studies were kept separately from the Delta score sheets.

Preparation of pollen grains for SEM photography

Pollen was scraped from anthers onto a microscope slide and flushed into a tube with 70% ethanol. The tube was vibrated in an ultrasonic bath for 5 min, the ethanol drawn off, and replaced with pure ethanol. Pollen grains were sucked from the tube with a clean eyedropper and deposited on a coverslip. This washing method removed a gluey coating from the pollen grain surface that obscured surface detail, and was much faster than acetolysis but less satisfactory in that the germ plasm projecting from the equatorial pores makes it difficult to find grains oriented to show the equatorial surface clearly. Coverslips were attached to an SEM mounting stub by electrically conducting graphite cement, the stubs sputter-coated with gold and examined in a Leica S440 SEM. SEM photos of New Zealand and South American *Gentianella* pollen grains were also available from two other sources: the Palynological Laboratory, Swedish Museum of Natural History, Stockholm, courtesy of Siwert Nilsson, and Landcare Research, Lincoln, courtesy of Neville Moar.

Preparation and examination of leaf cuticles

The epidermal cells leave a print on the thick leaf cuticle that can be photographed and analysed (Fig. 34). Strips of cuticles at least 3 mm wide were torn with forceps from the undersurface of a leaf. Cuticles were mounted in water and examined under the microscope. They were photographed at 100× and 250× using a green filter and PanX film. Prints were made to a uniform size to standardise measurements. The epidermal cell pattern was traced from the prints onto drafting film. Image analysis was done from these tracings, recording the shape factor for as many whole cells as were visible to the image analysis camera. The shape factor (S) is the ratio of the cell area to the perimeter length of the cell where a circle has a shape factor of one. The shape factor makes no distinction between elongated cells with straight walls and isodiametric cells with zig-zagged walls.

Stomatal guard cell length and the width across the two guard cells at mid-cell position was measured for all the cuticles examined and an area that encompasses the two guard cells and the stomatal gap was calculated as $((\text{length of the guard cells} + \text{width of both guard cells})/4)^2$, expressed in μm^2 using the mean from between three and eight stomata per specimen.

Preparation of transverse leaf sections

Pieces of leaf c. 5 × 5 mm preserved in FAA were cut from the leaf mid-lamina while immersed in water and put into Eppendorf tubes with FAA. Air was removed from the leaf sections by keeping them for 12 h under vacuum. The samples were put through an ethanol series and transferred to Technovit 7100 embedding resin (Kulzer Hist-Technik embedding kit) which was then set. Sections 5 µm thick were then cut and the sections stained with a methylene blue – azure blue mixture for 15–18 s and flushed with water. Sections were permanently mounted on slides using Depex.

Measurements (e.g., of leaf thickness) were taken from the area of the leaf between the midvein and the first lateral vein encountered in the section. These leaf sections proved to be of limited taxonomic value, and duplicate sampling from species was not done.

Chromosome numbers

The slide made of the Barrier Range gentian that gave a $2n = 18$ count is in the chromosome count slide voucher collection at Landcare Research, Lincoln. This was re-examined by M. I. Dawson to ensure no mistake had been made in the count. The specimen, unvouchered, was traced through Landcare Research, Lincoln, garden records to a collection from Lake Wapiti, collected by John Anderson of Albury in 1970 in the company of Alan Mark and John Salmon and grown for a time at Lincoln. John Anderson provided an exact locality for the gentians which were collected on that trip. New collections were made of all four gentian species present at Lake Wapiti and chromosome counts of these done by M. I. Dawson to test the reported count.

Measurement of seed dimensions

Shortest and longest diameters (called length and width) were measured from seeds that had been collected from the summer of 1997/8 or from earlier summers 1995/6 and 1996/7, using an image analyser (Metamorph version 3, with images captured by digital camera). Seed dimensions change as the seeds dry, and seed dimensions differ little between species. For these two reasons, very limited measuring of seed sizes was done.

Compilation of a morphological data matrix

A morphological data set suitable for cladistic analysis was compiled from the Delta data set using the Tonex program in Delta. This was then extended and modified to give a total of 31 characters (Table 5) for 45 taxa (Appendix). Maximum dimensions were used in the coding

of some quantitative characters (stem diameter, leaf petiole width, and flower length) to express the fully developed state in a species and to overcome the problem of very wide lower limits of plant parts. Stigma colour could not be obtained from dried specimens of the three South American species. The presence of female flowers where anthers are non-functional is difficult to determine from herbarium specimens, as large numbers of flowers need to be examined to detect it. The presence of female flowers was scored as uncertain for the South American and two Australian species. Adams (1995) observed gynodioecism in *G. diemensis* in Tasmania, and states that "partial or complete gynodioecy is probably widespread". I scored this species as having female flowers present.

Analysis was performed using the program Paup* version 4.0b2 for Macintosh (Swofford 1998) using the parsimony algorithm. A heuristic search under the Fitch parsimony assumption was conducted with starting trees obtained by random addition of the taxa with 10 000 replicates, tree bisection-reconnection branch swapping, and saving all of the 10 000 shortest trees. A strict consensus tree was obtained from these.

Table 5 Morphological characters and states used in parsimony analysis of *Gentianella*. All characters are unordered except for the sixth.

1. Life cycle: 0 = annual; 1 = biennial; 2 = perennial.
2. Caudex: 0 = unbranched, a single rosette; 1 = branched, with multiple rosettes.
3. Stolons: 0 = absent; 1 = present.
4. Dead leaf bases persisting: 0 = not persisting on caudex; 1 = persisting on caudex.
5. Flowering stem type: 0 = terminal and lateral; 1 = lateral only.
6. Rosette: 0 = absent from flowering plants; 1 = indistinct on flowering plants; 2 = distinct (ordered character).
7. Stem diameter: 0 = maximum stem diameter <5.0 mm; 1 = maximum stem diameter ≥5.0 mm.
8. Stem colour: 1 = green; 2 = crimson; 3 = purple-black; 4 = bronze.
9. Leaf colour: 0 = leaves without secondary pigments; 1 = crimson pigment; 2 = purple-black pigment.
10. Petiole width: 0 = maximum width <5.0 mm; 1 = maximum width ≥5.0 mm.
11. Leaf margins serrulate: 0 = smooth; 1 = minutely serrulate.
12. Leaf margin thickened: 0 = unthickened; 1 = thickened.
13. Pedicel number: 1 = one per axil; 2 = two or more per axil.
14. Calyx lobe shape: 0 = tapering; 1 = pandurate near the base.
15. Flower length: 0 = maximum flower length <15 mm; 1 = maximum flower length 15.0–19.9 mm; 2 = maximum flower length ≥20.0 mm.
16. Calyx margins: 0 = smooth; 1 = serrulate or papillose.
17. Calyx sinus hairs: 0 = absent; 1 = few; 2 = abundant.
18. Calyx lobe apices rounded: 0 = acute; 1 = rounded.
19. Corolla colour: 0 = absent; 1 = veins coloured red to blue; 2 = red-to-blue tinting present elsewhere than veins; 3 = yellow tinting present.
20. Corolla lobe sinus hairs: 0 = absent; 1 = present.
21. Nectary flap: 0 = absent; 1 = present.
22. Filament width: 0 = maximum filament width <1.5 mm wide; 1 = maximum filament width ≥1.5 mm wide.
23. Anther colour: 0 = yellow; 1 = purple-black; 2 = red (in *G. dianthoides* only).

24. Anther length: 0 = maximum anther length <1.5 mm; 1 = maximum anther length 1.5–3.0 mm; 2 = maximum anther length >3.0 mm.
25. Stigma colour: 0 = uncoloured; 1 = coloured blue or purple.
26. Leaf epidermis cell walls: 0 = non-zigzagged; 1 = zigzagged; 2 = thickened.
27. Palisade cells: 0 = absent; 1 = present.
28. Female flowers: 0 = never present, 1 = sometimes present.
29. Pollen surface pattern: 0 = striate; 1 = striate-reticulate; 2 = reticulate.
30. Callicolous: 0 = not callicolous; 1 = callicolous.
31. Distribution: 0 = South America; 9 = Australia; 1 = Subantarctic Islands; 2 = Stewart Island; 3 = Southland and Otago; 4 = Canterbury and Westland; 5 = Nelson and Marlborough; 6 = North Island.

DNA sequencing

ITS1 and ITS2 were sequenced for 21 species, including four South American species and four Australian species (Table 6). Total DNAs were isolated from fresh leaves of 24 individual plants. Four European species sequenced by Yuan & Küpfer (1995) and *G. magellanica* sequenced by Hagen & Kadereit (2001) were added to the data set.

Table 6 *Gentianella* specimens sampled for DNA sequences.

- G. antarctica*, C. Meurk, Campbell Island, CHR 510016, GenBank AY136501.
G. antipoda, G. Taylor, Antipodes Islands, CHR 510015, GenBank AY136400.
G. astonii, D. Glenny 6415, Isolated Creek, CHR 509942, GenBank AY136494.
G. bellidifolia, D. Glenny 6438, Red Hills, Nelson, CHR 590960, GenBank AY136490.
G. bellidifolia, D. Glenny 6297, Sanctuary Basin, CHR 509816, GenBank AY136498.
G. cerina, C. Meurk, Auckland Islands, CHR 510017, GenBank AY136502.
G. chathamica, P. J. de Lange CH21, Chatham Islands, CHR 510011, GenBank AY136495.
G. corymbifera, D. Glenny 6409, Mt Cook, CHR 509935, GenBank AY136493.
G. corymbifera, D. Glenny 6296, Culliford Basin, CHR 509815, GenBank AY136492.
G. grisebachii, B. Brown, Forgotten River Flats, CHR 510014, GenBank AY136489.
G. impressinervia, D. Glenny 6464, Kelly Saddle, CHR 509989, GenBank AY 136485.
G. lilliputiana, N. C. Simpson, St Bathans Range, CHR 542369, GenBank AY160218.
G. lineata, D. Glenny 6345, Mt Anglem, CHR 509866, GenBank AY136503.
G. montana var. *stolonifera*, D. Glenny 6418, Mt Davy, CHR 509944, GenBank AY136491.
G. saxosa, D. Glenny 6372, Big Bungaree Beach, Stewart Island, CHR 509898, GenBank AY136499.
G. serotina, D. Glenny 6381, Garvie Mountains, CHR 509907, GenBank AY136497.
G. spenceri, D. Glenny 6498, Mt French, Westland, CHR, GenBank AY136496.
- G. magellanica*, GenBank AJ294613 and AJ294673.
G. magellanica, P. Wardle & S. Wagstaff 97083, Argentina, Rio Negro, Cerro Catedral, CHR 514046, GenBank AY160219.
G. myriantha, S. Halloy 4271, Bolivia, Crop and Food germplasm accession 1404, voucher LPB, GenBank AY136488.
G. narcissoides, S. Halloy 4268, Bolivia, Crop and Food germplasm accession 1399, specimen voucher LPB, GenBank AY136486.
G. sp., S. Halloy 4285, Bolivia, Crop and Food germplasm accession 1413, specimen voucher LPB, GenBank AY136487.
- G. diemensis* subsp. *diemensis*, B. Brown, Tasmania, CHR 526451, GenBank AY136504.
G. polysperes, B. Brown, Tasmania, CHR 526450, GenBank AY136505.
G. pleurogynoides, B. Brown, Tasmania, CHR 526452, GenBank AY136506.

G. muelleriana subsp. *alpestris*, J. Ward 96048, Mt Kosciusko, Australia, CHR 526435, GenBank AY136507.

G. biebersteinii, GenBank Z48147 and Z48126.

G. caucasea, GenBank Z48101 and Z48127.

G. campestris, GenBank Z48104 and Z48128.

G. umbellata, GenBank Z48102 and Z48132.

Total DNA was extracted from leaves using the CTAB method of Doyle & Doyle (1987) and suspended in 100 μ l of TLE buffer. DNA in the ITS region was amplified in two steps. Double stranded DNAs of the complete ITS region in each genomic DNA were amplified using primers ITS 28CC (5'CGC CGT TAC TAG GGG AAT CCT TGT AAG 3') and ITS 18D (5' CAC ACC GCC CGT CGC TCC TAC CGA TTG3'). PCR were done with 1 μ l of the suspended total DNA, 5 μ l of Taq polymerase reaction buffer, 4 μ l of 5mM dNTP, 2 μ l each of primers 28CC and 18D, 0.25 μ l of Taq DNA polymerase (Boehringer Mannheim) and 36 μ l of double-distilled water. The thermal cycling was done in a Perkin-Elmer thermal cycler for 30 cycles with the following conditions: 97°C for 1 m, 52°C for 1 m, 72°C for 45 s with an extension of 4 s per cycle. Single stranded DNAs were amplified using the same primers. PCR were conducted for 15 cycles, with 10 μ l of template DNA, other quantities double that used for double stranded amplification. Primers and excess salts were removed by alcohol precipitation in the presence of ammonium acetate. The single stranded fragments were sequenced by the dideoxy method using Sequenase (version 2.0, U.S. Biochemical), and four internal primers ITS18 (5' GTT TCC GTA GGT GAA CCT GC 3'), ITS3, ITS2 and ITS4 (White et al. 1990). These fragments were electrophoresed on 5% acrylamide gels and made visible on X-ray film by autoradiography.

Boundaries of the spacer regions were determined by comparison with the sequences of Yuan & Küpfer (1995) for *Gentianella*. The sequence of each species was manually aligned by sequential pairwise comparisons and was confirmed by reading the complementary strands.

Analysis was performed using the program Paup* version 4.0b2 for Macintosh (Swofford 1998) using the parsimony algorithm. A heuristic search under the Fitch parsimony assumption was conducted with starting trees obtained by random addition of the taxa with 10 000 replicates, tree bisection-reconnection branch swapping, and saving all of the 10 000 shortest trees. A strict consensus tree was obtained from these.

Analysis was also done with Spectronet (Huber et al. in press, Langton & White 2001), a phylogenetic analysis program that shows ambiguity in data by means of a network. Because Spectronet excludes characters where there are any missing bases for any species,

missing bases were replaced with the base that is in common to all species or to most species so as not to introduce new information to the sequences.

Yuan & Küpfer (1995) established a broad phylogeny for the Gentianaceae. Adding the Southern Hemisphere sequences to Yuan & Küpfer's data set made it clear that the Northern Hemisphere *Gentianella* species they sampled (i.e., *G. caucasea*, *G. biebsteinii*, *G. umbellata*, and *G. campestris*), could be used as an outgroup to the Southern Hemisphere species, as the Australasian species were nested within European *Gentianella*.

CHARACTERS

Description of morphological characters

The following characters were used in the species descriptions and various analyses reported in the Results section.

Monocarpic plants flower and set seed once then die. This condition may be distinguished by the presence of a terminal flowering stem that is usually more robust than any laterals, and the complete absence in plants forming a population of dead flowering stems. Dead plants that flowered in the previous season will be present in the area, as will be rosette plants. Rosette plants are plants which have not yet developed flowering stems. The monocarpic state includes *annuals* and *biennials*. Adams (1995) used the term *plietesial* for plants that are monocarpic and flower once sufficient resources are accumulated. I have called these facultative biennials. Some New Zealand species may be of this type, but this would be difficult to determine without monitoring over several years.

Annuals are monocarpic plants that complete their life cycle within a 12 month period. Such plants have a small root system, and vary considerably in size at flowering time, as every plant flowers regardless of its size. In the field, the state may be distinguished from bienniality by the lack of rosette plants at flowering time.

Biennial plants flower in the season following the one in which that they grow from seed. In populations of biennial plants, three states can be seen: rosette plants that are not flowering in the current season, flowering plants flowering in the current season, and dead plants that flowered in the previous season will be present. The rosette plants will be present in equal numbers to flowering plants. The first season's rosette leaves may die over the winter or in the next growing season but are replaced the following summer. The rosette leaves of the rosette plant are commonly larger than those of the flowering plant.

Polycarpic plants flower in successive years and may be distinguished by the presence of dead flowering stems on living plants, and a well developed and often much branched caudex. Polycarpic plants do lose their green colour at the end of the flowering season. Dead plants and rosette plants are a small percentage of those seen.

Most species are fixed in their monocarpy or polycarpy, but some species (e.g., *G. patula*, *G. corymbifera*, and *G. montana*) are not, and this polymorphism tends to have a geographic basis, e.g., *G. corymbifera* is sometimes polycarpic in Nelson but not elsewhere. Simpson & Webb (1980) reported occasional polycarpy for *G. divisa*.

Height in flower was measured from ground level to the tips of the flowers. This

height will be the same as the length of the flowering stems where they are erect, but where the branches are decumbent, it will be less than the length of some of the branches.

Roots were scored as branched or unbranched in an attempt to correlated root system type with growth habit, but this appears to be of no taxonomic value as all species seem to be tap-rooted and the root divides where there is an obstruction. Root diameter was measured at the caudex base, and is only occasionally of taxonomic value.

The *caudex* is the main stem and may be unbranched and short, or branched and then usually long and distinct. It is distinguished from the root by the presence of leaf scars and by being usually crimson coloured while the root is usually yellow. This distinction is sometimes unclear and unscarred crimson tissue can be difficult to assign to stem or root. Where the caudex is branched, it is measured from the top of the root to the base of the leaf rosettes on each branch, if they are distinct. In *G. astonii*, which has no distinct rosettes on the branches, no distinction between caudex and flowering stem can be made. Most monocarpic species have a caudex too small to be measured. An exception is *G. antipoda*, a biennial (Godley 1982), which has a branched caudex with the branches c. 100 mm long with leaf scars along bare branches).

Monocarpic species always have a terminal *flowering stem* which arises from the apex of the central rosette of leaves. In small monocarpic plants, there is often only a single terminal flowering stem. On larger individuals, lateral branches appear, either from the axils of rosette leaves or from low on the terminal flowering stem. There is no absolute distinction possible between lateral flowering stems and what can be considered to be branches of a single flowering stem arising from flowering stem bracts, making the number of lateral flowering stems a somewhat arbitrary figure. In *G. divisa*, for instance, in some plants the number of flowering stems can be counted without any difficulty, while in others an attempt to assign a number is meaningless.

In polycarpic species the flowering stems may be both terminal and lateral as in monocarpic species, or lateral only, with a flowering stem never arising from the terminal rosette of the plant or one of its non-flowering branches. Lateral-only branching defines a group of species that includes *G. bellidifolia* and *G. astonii*. Sometimes secondary branching is well developed, a feature of *G. astonii*, *G. saxosa* and *G. concinna*.

A few species are able to sprout new branches from old parts of the caudex. These are referred to here as "stolons" in accordance with existing New Zealand literature, (e.g., *Gentiana montana* var. *stolonifera* was diagnosed as having a "stem with long creeping stolons at the base" — Cheeseman 1925) but they could be called more accurately

"adventitious branches". They are only seen in the *G. montana* species group.

The shape, size, thickness, and folding of the leaves offer valuable characters to distinguish species, but can only be seen on fresh plants. The shape describes the lamina above the petiole. The petiole is well defined in some species but not in many others, and this distinctness or lack of it was scored as a character. Where the petiole is indistinct, it is difficult to define the lamina length in a way that is comparable to cases where it is distinct. As a result, leaf shape and petiole length are sometimes only approximate. To have based the leaf shape on the complete leaf would have resulting in only two basic shapes, linear to narrowly elliptical and spatulate to narrowly spatulate. The distinction between elliptical, narrowly elliptical, and linear follows Stearn (1983, fig 19) with modifications. Stearn defines linear as a leaf with a length to width ratio of 12:1, narrowly elliptical as a ratio of 6:1 to 3:1, elliptical as a ratio of 2:1 to 3:2, broadly elliptical as a ratio of 6:5, and circular as 1:1. Since these definitions do not define all leaf length to width ratios (e.g., those between 6:1 and 12:1), I have defined these terms more comprehensively as follows: linear: a length to width ratio of $>9:1$; narrowly elliptical: a ratio of $9:1$ – $2.5:1$; elliptical: a ratio of 2.5 – $1.2:1$. I omitted the term broadly elliptical, and defined orbicular leaves as having a ratio of 1.2 – $1.0:1$.

Rosette leaf length includes the petiole, and leaf width is measured at the widest point of the leaf. In using keys and descriptions, the largest leaf from a flowering plant's rosette should be used.

A rosette leaf may be folded in one of two ways: in transverse section it can be V-shaped or U-shaped (referred to as channelled) and this refers to the lamina, not the petiole. The midvein usually projects from the abaxial leaf surface. Channelling of the petiole is more common than that of the whole leaf, and intermediates exist, making the character somewhat subjective.

Rosette leaves are sometimes rigidly recurved, particularly when the leaf is folded, as opposed to being flat and assuming a curved shape due to gravity. This rigidly recurved shape has been scored as present or absent.

Petiole width was measured at the narrowest point of the the leaf near the leaf base. Where the petiole was strongly channelled, the measurement was taken from a petiole that was flattened as much as possible without breaking the petiole.

Lateral flowering stems were subjectively scored as erect or decumbent, but all intermediates exist.

Flowering stem diameter was measured from the terminal flowering stem just above the

rosette of leaves, or in lateral flowering stems, near their origin from a leaf axil. The diameter was measured on fresh and dried specimens to make it possible to use this character when identifying dried plants. When stems dry, they shrink on average by one third.

Flowering stem colour was scored as a multi-state character. Secondary pigments may be completely absent. Crimson and purple-black tinting usually appeared distinct and may involve a different pigment. A bronze coloration is also sometimes seen, and may result from presence of the crimson pigment and a yellow-green pigment. The same multi-state character was used for flowering stems, rosette leaves, and calyces, but the distribution of pigments varies and separate characters are needed for the three parts.

The number of flowering stem leaf pairs was estimated, but it is often a subjective decision what to count as rosette leaves and flowering stem leaves. Where there is no distinct rosette, and the leaves grade from the base to the upper inflorescence, the number is not very meaningful, but I have provided it in all cases to make descriptions comparable.

The absence of a rosette in flowering plants is a conspicuous feature of *G. grisebachii* and was therefore scored. In this species, the internodes between rosette leaves elongate to some degree, so that there is no condensation of leaves at the plant base. Leaf measurements are taken from the lowermost leaves.

Flowering stem leaves are similar to the rosette leaves but are increasingly sessile and decrease in size with increasing distance along the flowering stem. They sometimes contribute to the characteristic appearance to the plant, but I was unable to find a way of scoring them as a multi-state character because of the difficulty of finding standard positions to measure these leaves, the only such position available being the bract subtending the terminal pedicel.

The position of the lowest flowers on the flowering stem is characteristic for some species (for instance, it is always low in *G. chathamica* and *G. spenceri*) but is variable in others (e.g., *G. corymbifera*). This was scored as one of three states: near the base of the stem, at mid-stem or near the stem apex.

The *number of pedicels* that originate at a bract axil is either one or two, rarely three. The regular presence of paired pedicels is a characteristic of some species. Paired pedicels occur in most members of the *G. saxosa* and *G. montana* groups, but also in the larger species of the *G. spenceri*, *G. bellidifolia* and *G. divisa* groups. It is completely absent from the *G. grisebachii* group and *G. astonii* complex. Nodes are sometimes very condensed giving the appearance that paired pedicels originate from a single axil when actually there

are two axils involved.

Pedicle length was measured during the male phase of the flower terminating that pedicel. Pedicels have a characteristic length in some species (e.g., short in *G. spenceri*), and elongate greatly after flowering in some species (e.g., in *G. grisebachii*). This tendency to elongate after flowering was not systematically scored.

Pedicle diameter can be measured at any point on the pedicel as it is usually uniform in width. The pedicel is square in section and the distance was measured between opposite faces. This diameter was measured from both fresh and dried specimens as for flowering stem diameter.

In *Gentianella*, plants usually have hermaphroditic flowers. Burrows & Hobbs (1964) noted gynodioecy in a population of *G. bellidifolia* at Arthur's Pass. Gynodioecy is the state where some plants in a population have hermaphrodite flowers while others have female flowers (Webb et al. 1988). This is a rare state for any population in New Zealand *Gentianella* and no species is gynodioecious through its range. A much more common phenomenon in New Zealand *Gentianella* species is that, in some flowers on a plant, the anthers are non-functional. It is common only in *G. divisa* and *G. filipes* and is sometimes a late-season phenomenon. Burrows & Hobbs (1964) observed that the corolla in female flowers of *G. bellidifolia* was smaller, and this is also sometimes true for sporadically occurring female flowers.

Flower number per plant is correlated to plant size and the number of flowering stems, but is useful as a more objective measure than flowering stem number. I avoided using Adams' (1995) measure of the number of flowers in the "primary partial inflorescence" or "terminal partial inflorescence" as this requires a subjective judgement of what constitutes the partial inflorescence.

All but one species of New Zealand *Gentianella* are 5-merous, although plants with individual flowers with 4, 6 or 7 calyx lobes may be found. These are not uncommon in *G. divisa*. *G. lilliputiana* is exceptional in being uniformly 4-merous.

Flower dimensions and pedicel lengths were measured only from flowers in male phase. Fig. 1 shows changes in four selected floral dimensions over 16 days for a single flower of *G. stellata* in the glasshouse (Figures for each chapter are at the end of the chapter). The male phase marked by anthesis started on the second day and lasted for 8 days. The female phase started on the 10th day. The corolla started to shrivel on the 16th day. Calyx length and filament length are most constant during the male phase. Corolla length and ovary length increase dramatically in the female phase (Table 7).

Table 7 Changes in length of pedicel and floral parts with flower age in *Gentianella stellata* from a single flower.

Flower part	% increase during male phase	% increase during female phase
Pedicel	0	31
Calyx	0	15
Corolla	13	24

Flower length was measured on flowers from the corolla tips to the base of the calyx, this lower point sometimes difficult to establish exactly, but as it does not involve dissection, the measurement is easily made. Flower diameter has been used elsewhere (e.g., Adams 1995) but is not available from pressed flowers, and depends on the degree of opening of the corolla.

The form of the *calyx* does not differ substantially within the genus, but differences in the degree of lobing and shape of the lobes make the calyx one of the most taxonomically useful parts of the plant (Fig. 4–8). *G. gibbsii* has the most deeply lobed calyx (c. $\times 0.89$) while *G. corymbifera* ($\times 0.29$ – 0.54) and *G. lilliputiana* (c. $\times 0.4$ – 0.5) are the most shallowly lobed. *Calyx length* was measured from the calyx lobe tips to the fusion line of corolla and calyx. This measurement involves removal of the calyx from the corolla to find the fusion line (the fusion line can be seen in Fig. 4–8). *Calyx lobe length* is measured from the calyx lobe tips to a point midway between the sinuses. *Lobe width* is unequal in most species to varying degrees, with two lobes at positions 10 and 2 o'clock being larger and overlapping the other three lobes; the one between these I call the apical lobe (at 12 o'clock) and two "tails" are at 5 and 7 o'clock (cf. *G. antarctica* in Fig. 4). Extra calyx lobes appear at 6 o'clock. The ratio of the largest lobes to the apical lobe is sometimes characteristic, and was scored as a character. It has not been incorporated into the keys and descriptions but is conveyed in the illustrations of the calyces. *Calyx lobe colour* was scored as green, purple-black, or bronze. *Recurved calyx lobes* occur in species that also have recurved leaves. Most *calyx lobe apices* are acute, but rounded apices occur in some species of the *G. saxosa* group. *Calyx lobe margins* may have projecting cells that appear as papillae, or if the cells are very large, the leaf margin appears minutely serrulate under the dissecting microscope. The *calyx lobe sinus* is usually acute, but is rounded in some species. This feature was used as the first character by Allan (1961) in his key to the New Zealand gentians to distinguish *G. astonii*, *G. saxosa*, *G. tenuifolia*, *G. corymbifera*, and *G. serotina* from the remainder of the species but intermediates exist (e.g., *G. divisa* — Fig. 5) and it is not constant for a

species, making it an unsatisfactory character. I have not scored it. The larger two calyx lobes are attached at their base within the adjacent lobes in some species, by as much as 1.0 mm of overlap. This seems to be particularly characteristic of the *G. montana* and *G. bellidifolia* species groups, but occurs to varying degrees in other species. It was not scored but is conveyed in the calyx illustrations. The calyx lobe ratio was derived from calyx lobe width divided by lobe length, but is only used in the *G. bellidifolia* group PCA.

Calyx sinus hairs are present in most but not all species, and their presence is a valuable character, but can only be seen in fresh or FAA-preserved specimens. The hairs are tiny (c. 0.2 mm long), are sometimes black-tipped, and were scored as absent, few (1–3) or abundant (4–8). Hairs also occur inside the calyx where they are scattered below the level of the sinus and are often denser at the fusion line between calyx and corolla. The presence or absence of these hairs appears to be of no taxonomic value.

The morphology of the *corolla* of New Zealand *Gentianella* is shown in Fig. 8. The corolla of most South American and Australasian *Gentianella* species differs from that of the Northern Hemisphere species in being more deeply lobed and lacking a fringe of hairs or laciniae on the inside of the corolla on a line between the sinuses.

Corolla colour was divided into a 3-state character: white / white with coloured veins / coloured in other parts of the corolla than in the veins. The colour found in the corolla is usually some shade of crimson or purple (illustrated in *Gentianella tenuifolia* and the Cobb gentian by Malcolm & Malcolm 1988, p. 107), but may be violet, or what Adams (1995) called "grey-violet" (illustrated in *Gentianella muelleriana* ssp. *alpestris* by Costin et al. 2000, p. 171). In the Subantarctic gentians, the colour is sometimes a blue close to ultramarine without any admixture of red (e.g., in *G. cerina*, *C. Meurk*, Enderby Island, CHR 510018). Godley (1982) describes the many ways in which colour may be distributed in the corolla. The colour varies in intensity and in extent from coloured veins or corolla lobe apices to uniform colouring throughout the corolla. Corolla colour is correlated to some extent with stigma colour, but coloured stigmas occur in some white-flowered species (e.g., in *G. divisa*). A yellow pigment is present in the corolla of some species. *G. impressinervia* has yellow at the base of the corolla and the corolla of *G. luteoalba* is uniformly a pale yellow. The corolla tube may be distinctly green (e.g., in some populations of *G. montana* var. *stolonifera*).

Corolla length was measured after the calyx was removed, and taken from the base of the corolla (where the ovary joins the corolla) to the corolla lobe apices. *Corolla tube length* is the length from corolla base to the sinuses between the corolla lobes. *Corolla lobe*

length was measured from a point midway between the sinuses to the corolla lobe apices. The width was measured at the widest point of the lobe.

Multicellular hairs are usually present on the inside of the corolla in a small area between the base of the corolla lobe sinuses and the point of attachment of the anther filament. These hairs are presumably a reduction of the fringe inside the corolla at this level that is found in Northern Hemisphere species of *Gentianella*. They are absent in only a few New Zealand species. They are usually almost straight, but in *G. calcis* subsp. *manahune* they are curled and twisted.

The distance from the base of the corolla to the base of the nectary pocket was measured. The shape of the swelling that defines the nectary varies between a V-shape and a U-shape, and the swelling varies in prominence, but neither feature was systematically recorded. Where this swelling became extended into a flap of tissue, it was noted.

Filament length was measured from the base of the corolla to the top of the filament. The filaments grow rapidly in length just before bud opening, and flowers in bud cannot be used for this measurement. *Filament width* was measured at the widest point of the filament on fresh or rehydrated flowers. The filament is fused to the corolla for about half of its length and the widest point of the filament is always at the point at which they become free. This width is strongly correlated with anther size, as might be expected for a structure that supports the anther. Filaments differ significantly in width between species. Filaments are widest in *G. divisa*, *G. amabilis*, *G. bellidifolia*, and *G. impressinervia* (up to 1.6–2.4 mm wide). They are narrowest in *G. antipoda*, *G. antarctica*, *G. astonii*, *G. chathamica*, *G. grisebachii*, and *G. lineata* (as narrow as 0.3–0.5 mm). Filament width is a more useful taxonomic character than filament length which is strongly correlated with corolla length.

Anthers are versatile. In the bud they face the ovary (introrse), and turn to face the corolla (extrorse) at the time of opening of the flower in most species. However, in three species, *G. chathamica*, *G. gibbsii*, and *G. lineata* and sometimes in other species, particularly *G. grisebachii*, this change does not take place, or may be partial (the anthers are then more or less horizontal). The character has to be assessed in the field or soon after collection.

Anther length was measured from fresh anthers that had not dehisced, as anthers shrink after dehiscence. Rehydrating flowers in hot water reinflates the anthers to their original size. *Anther wall colour* was scored as a multi-state character. Purple-black anthers are the norm, but anthers with no pigment in the walls appear yellow. This is a constant feature of *G. stellata*. It is seen in the Waima Valley populations of *G. astonii* subsp. *astonii*, in *G.*

corymbifera in North Canterbury, Marlborough, and Skippers Creek in Otago, and occurs occasionally in *G. antarctica* and *G. antipoda* (Godley 1982). A few species (e.g., *G. spenceri*) appear to have a different pigment that appears as a dark red colour. There is usually a few rows of cells near the line of dehiscence of the anther which lacks the gentian violet found in the other cells. I have termed this the anther mouth. Where anther walls are dark red, the mouth appears orange-red.

Pollen diameter was measured in the early stages of the revision but seemed to have no taxonomic value and has been omitted from the descriptions. Pollen appears yellow under the light microscope, but may appear to be pink, orange, or black due to staining from the anther wall. Because this staining is so constant in species where it occurs it was scored as a character. Adams (1995) noted that "dimorphism in pollen grain shape seems to be common in many species". I have not seen this in any New Zealand species.

The ovary in the New Zealand gentians is almost sessile, and there is no style, the stigma dividing immediately at the top of the ovary. *Stigma colour* can be seen only in fresh flowers. The outer ovary wall is usually yellow, but the cells that make up the stigmatic surface are themselves usually uncoloured. However, a crimson, blue, purple, or violet tinting is sometimes present which is always present in some species (e.g., *G. spenceri*), or may be present in only some populations (e.g., in *G. divisa*). Ovary colour during the phase of seed development was scored for some species as it changes in some species from yellow to a blue or purple colour. Too few plants at this phase were available to determine the taxonomic value of this colour change.

The *ovules* are in four rows and are attached to the inside surface of the outer ovary wall near the two vertical suture lines. The ovules were usually counted in immature ovaries. In most flowers, all the ovules develop to become seeds. The number of ovules per row is quite variable within a species (e.g., 5–20 rows in *G. bellidifolia*) but differences between species are often significant. For example, *G. antipoda* has a lower ovule number than *G. antarctica* (Godley 1982). The ovary length increases with maturity and was not measured. Instead, *capsule length* offered a standardized measure of ovary length since it represents the length of the mature ovary. It was measured from the base of the corolla to a point midway between the tips of the ovary. The measurement is shorter than if the curved tips of the capsule mouth were straightened, a difference significant in the short capsules of the two annual species.

Seed colour varies within a very small range that requires colour charts to be used for discrimination, all being close to 5YR 4/2 in the Munsell colour system (Munsell Color

1977) and were therefore not recorded. Seed size varies little between species, but seeds shrink with age due to dehydration.

New Zealand distribution is by land district. The land district boundaries are shown in the New Zealand flora series endpapers (e.g., Allan 1961) and in more detail in the *New Zealand Descriptive Atlas* (McLintock 1959).

Variation in quantitative characters used in analyses

For three *Gentianella* species, nine quantitative characters were studied, using all measurements of these taken from fresh plants for the data sheets from which were produced the species descriptions. The characters analysed were plant height, leaf length, leaf width, flower number, petiole width, calyx length, corolla length, filament length, and anther length. The species studied were *G. corymbifera*, *G. montana*, and *G. vernicosa*, representing both widespread and variable species and localised less variable species.

The results (Table 8) confirm Stace's (1980) demonstration that vegetative parts show greater variation than floral parts. In these three species variation in floral parts was less than variation in vegetative parts by a factor of two. The only character that measures numbers of parts is number of flowers, and this is particularly variable. The variability of *G. corymbifera* exceeds the other two species in all characters, and reflects geographical variation which is particularly marked in this species.

For the same three species, six characters were tested for normality. The goodness of fit to a normal distribution using the χ -square test was used (Table 9) and shows that these characters rarely depart from normality ($p = 0.95$) as only anther length in two species failed to conform to a normal distribution. Maximum and minimum values derived from the sample mean and standard deviation have a good chance of reflecting the true variation in each character.

Levels of significance for comparisons of means using the t-tests presented in the Results are: *** = 99.5%, ** = 97.5%, * = 95%. The levels of significance have been set unusually high to compensate for the large numbers of comparisons done. For the largest comparison of means involving 16 comparisons, there is a probability of 7.3% that one comparison will be significant at the 99.5% level by chance alone (calculated from the binomial distribution for $n = 16$, $p = 0.005$, $k = 1$). But the probability that two or more comparisons at this level will occur by chance alone is only 0.3% ($n = 16$, $p = 0.005$, $k \leq 2$).

Table 8 Coefficients of variation in quantitative characters in three New Zealand gentian species.

	<i>G. corymbifera</i>	<i>G. vernicosa</i>	<i>G. montana</i>
plant height (mm)	48% (n = 29)	40.6% (n = 22)	35.1% (n = 43)
leaf length (mm)	42% (n = 41)	25% (n = 25)	30.4% (n = 39)
leaf width (mm)	45% (n = 39)	25.6% (n = 24)	21.5% (n = 36)
petiole width (mm)	59% (n = 25)	27.4% (n = 16)	42% (n = 39)
flower number	83% (n = 21)	67% (n = 22)	67% (n = 35)
corolla length (mm)	18% (n = 22)	14.7% (n = 7)	11.3% (n = 20)
calyx length (mm)	24% (n = 29)	13.9% (n = 13)	14.7% (n = 17)
anther length (mm)	14% (n = 24)	17.7% (n = 10)	10.9% (n = 25)
filament length (mm)	21% (n = 26)	10.3% (n = 8)	12.7% (n = 19)

Table 9 Test for normal distribution in three species and eight characters using χ -square test.

	<i>G. corymbifera</i>			<i>G. montana</i>			<i>G. vernicosa</i>		
	χ -square	d.f.	p	χ -square	d.f.	p	χ -square	d.f.	p
leaf length	11.3	26	0.99	7.9	30	1	7.9	30	1
leaf width	12.3	28	0.99	7.9	29	1	7.9	29	1
petiole width	4.3	28	1	6.3	30	1	6.3	30	1
corolla length	5.1	22	1	3.1	31	1	4.1	31	1
anther length	8.5	13	0.82	14.8	20	0.79	4.6	18	1
calyx length	4.6	19	1	4	21	1	6	17	0.99
plant height	6.7	15	0.96	2.4	15	1	3.9	18	1
flower number	1.6	19	1	3.8	13	0.99	2.5	17	1
filament length	2.1	17	1	3.6	12	0.99	2	11	0.99

Deriving minima and maxima and how many measurements are sufficient to make these reliable

Maximum and minimum values are used a great deal in plant taxonomy, both in keys and descriptions. The inner and outer limits are expressed in the form (a-)b-c(-d) where a and d are the outer limits and b and c the inner limits. I have used the outer limits to give the extremes that I have found in all measurements taken from specimens, and estimated the inner limits from the data as including most of the specimens. Where I have done statistical analysis of a character for a species, I give the range in the form (a-)b-c-d(-e) where c is the sample mean from a data set.

To estimate how many specimens were needed to derive these minima and maxima, I wrote a program in Pascal that would accept a sample mean and sample standard deviation and a number of "samples" (between 0 and 40) were derived by the program that conformed to normal distribution with those two parameters. Modelling the behaviour of such a statistical distribution in a particular circumstance is called a Monte Carlo trial as it involves large repetitions of the same statistical algorithm. The minimum and maximum from these "samples" were then compared with maximum and minimum values derived from 1 000 generated "samples". An error rate was calculated for the initial sample number by calculating how many of the 1 000 samples lay outside the initial minimum and maximum. The results are presented in Fig. 2-3. Corolla length in *G. vernicosa* is under tight genetic control and the coefficient of variation is only 18%. The number of measurements needed on average to derive a range that will encompass 95% of specimens is 28. The number of flowers per plant in the variable *G. montana* is influenced by plant size and age and the coefficient of variation is 67%. Surprisingly however, to derive a range that will encompass 95% of specimens, only 34 measurements will achieve this on average, and assuming that the character conforms to the normal distribution. Most characters will lie between these two extremes, and the number of specimens that are needed to derive ranges that are reasonably accurate is between 25 and 35 specimens.

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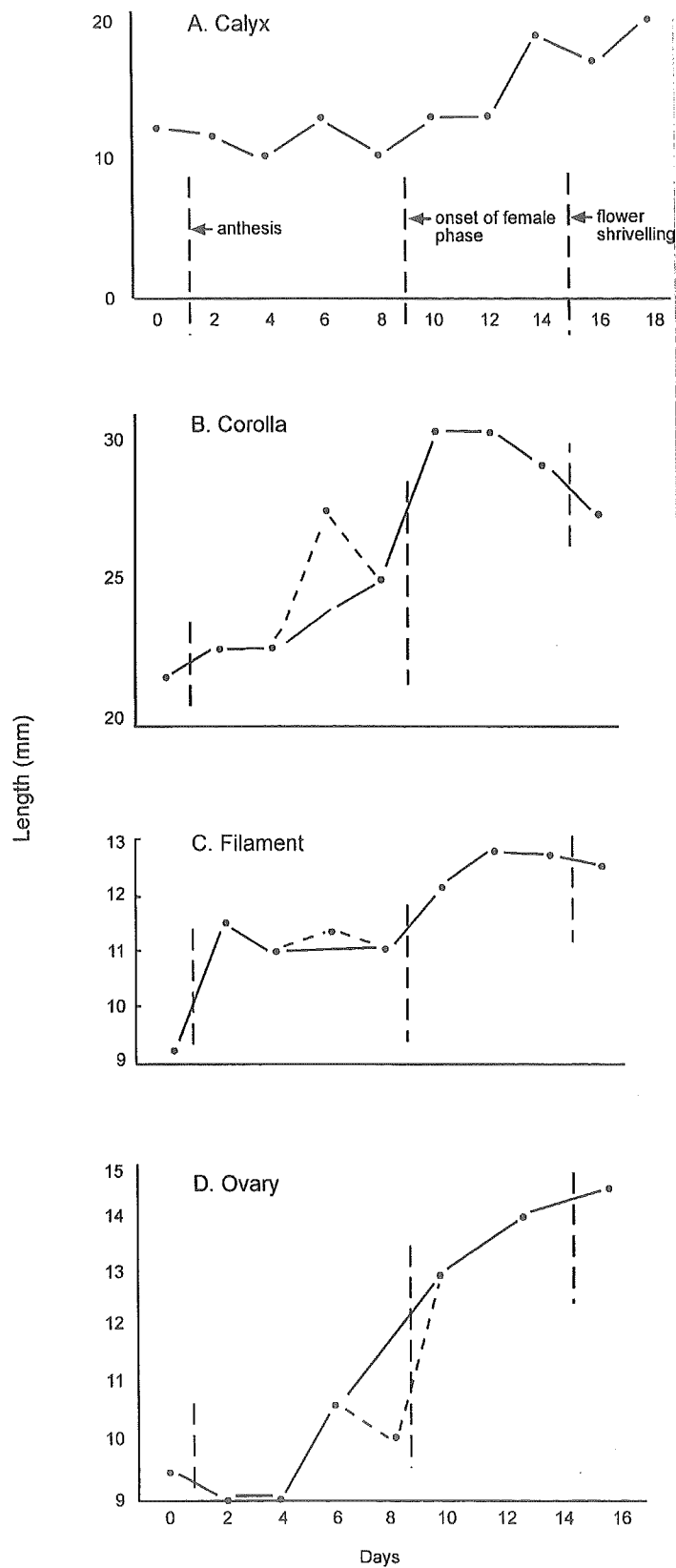


Fig. 1 Changes in floral dimensions in a single flower of *Gentianella stellata* over 16 days.

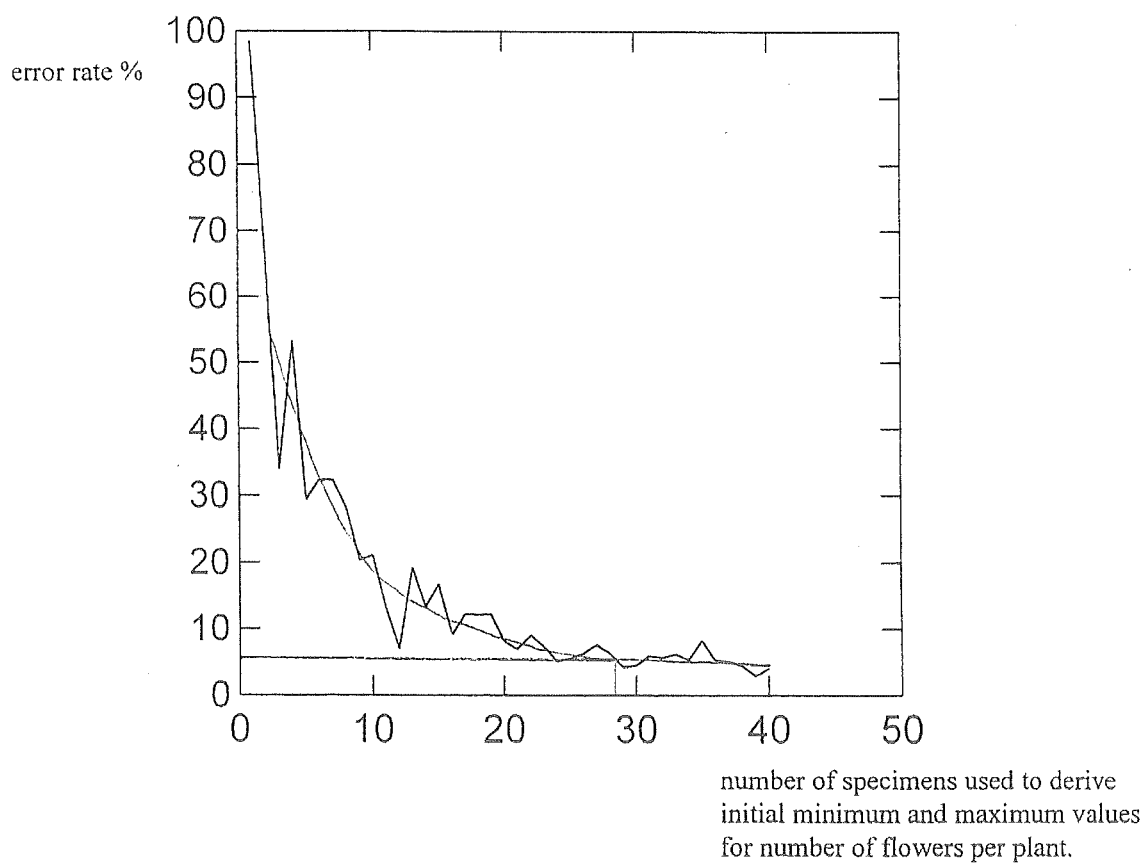


Fig. 2 Results of Monte Carlo trial using sample mean and standard deviation for corolla length in *Gentianella vernicosa* where $\bar{X} = 14.9$ mm, $s = 2.2$ and coefficient of variation 18%. The error rate declines sharply as more specimens are used to derive minimum and maximum. The number of specimens needed to derive a minimum and maximum with an error rate of 5% is c. 28. Curve smoothed by eye.

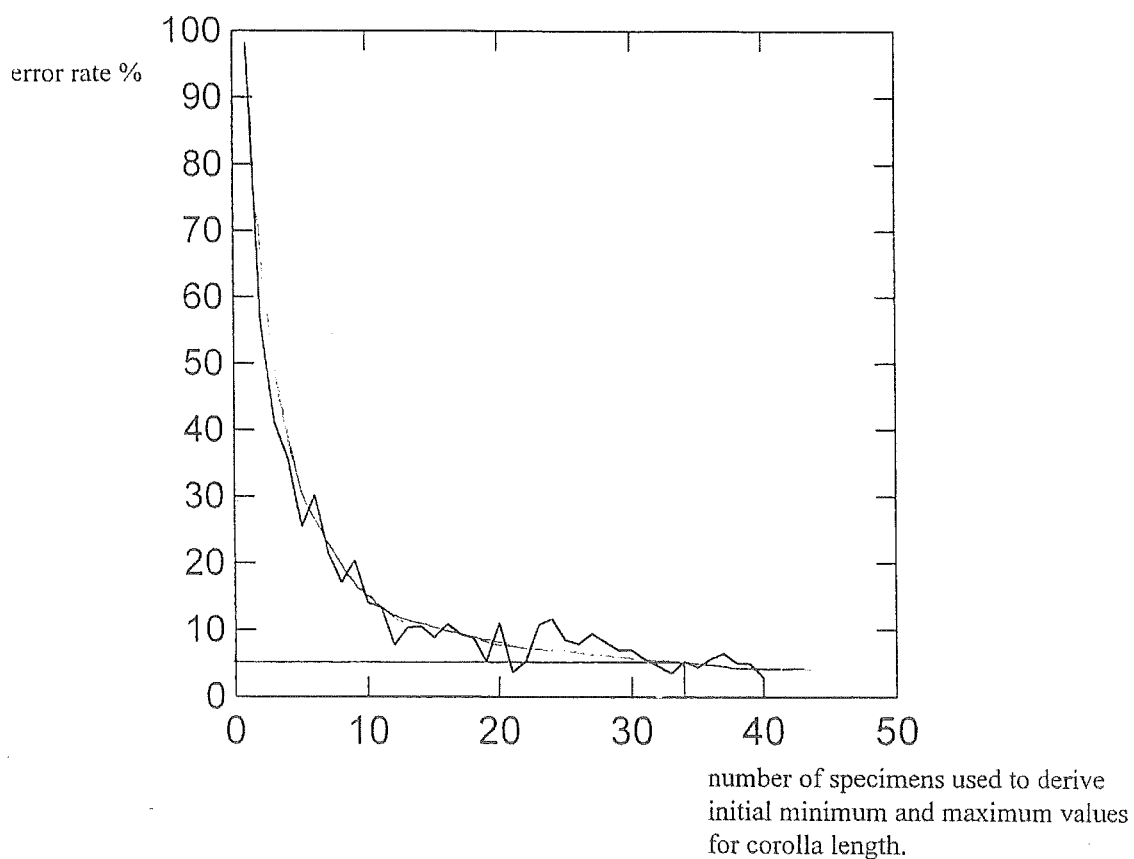


Fig. 3 Results of Monte Carlo trial using sample mean and standard deviation for number of flowers per plant in *Gentianella montana s. l.* where $X = 21.4$, $s = 14.3$, and coefficient of variation 67%. The error rate declines sharply as more specimens are used to derive minimum and maximum. The number of specimens needed to derive a minimum and maximum with an error rate of 5% is c. 34. Curve smoothed by eye.

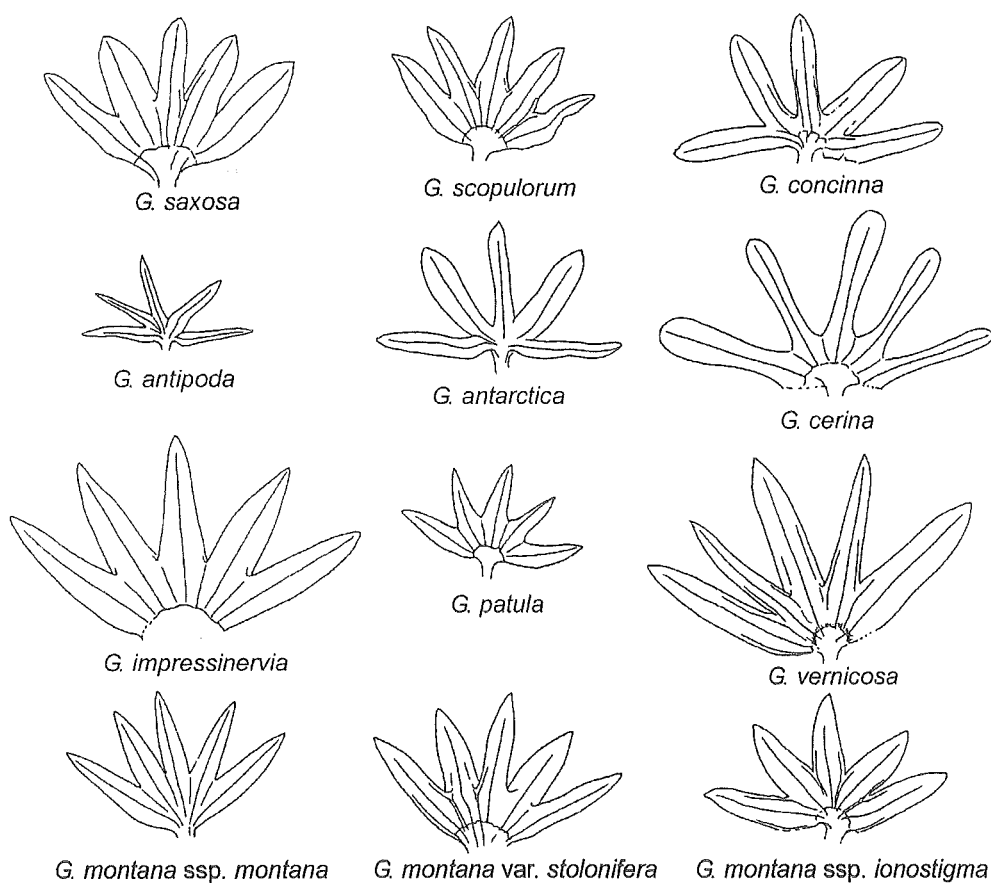


Fig. 4 Calyces of the *Gentianella saxosa* and *G. montana* groups.

G. saxosa group: *G. saxosa*: S. G. Royds, Bluff, CHR 191762; *G. scopulorum*: D. Glenny 6326, Charleston, CHR 509848; *G. concinna*: C. Meurk, Auckland Is., CHR 526412; *G. antipoda*: E. J. Godley, Antipodes Is., CHR 549027; *G. antarctica*: E. J. Godley, Campbell Is., CHR 549028; *G. cerina*: C. Meurk, Auckland Is., CHR 510017. *G. montana* group: *G. impressinervia*: G. Jane, Mt Mantell, CHR 516245; *G. patula*: D. Glenny 7428, St Arnaud Range, CHR 560059; *G. vernicosa*: D. Glenny 7432, Cundy Creek, CHR 560061; *G. montana* ssp. *montana*: P. N. Johnson 1358, Borland Saddle, CHR 511786; *G. montana* var. *stolonifera*: D. Glenny 6418, Sewell Peak, CHR 509944; *G. montana* ssp. *ionostigma*: I. Breitwieser 2062, Mt Hikurangi, CHR 526397.

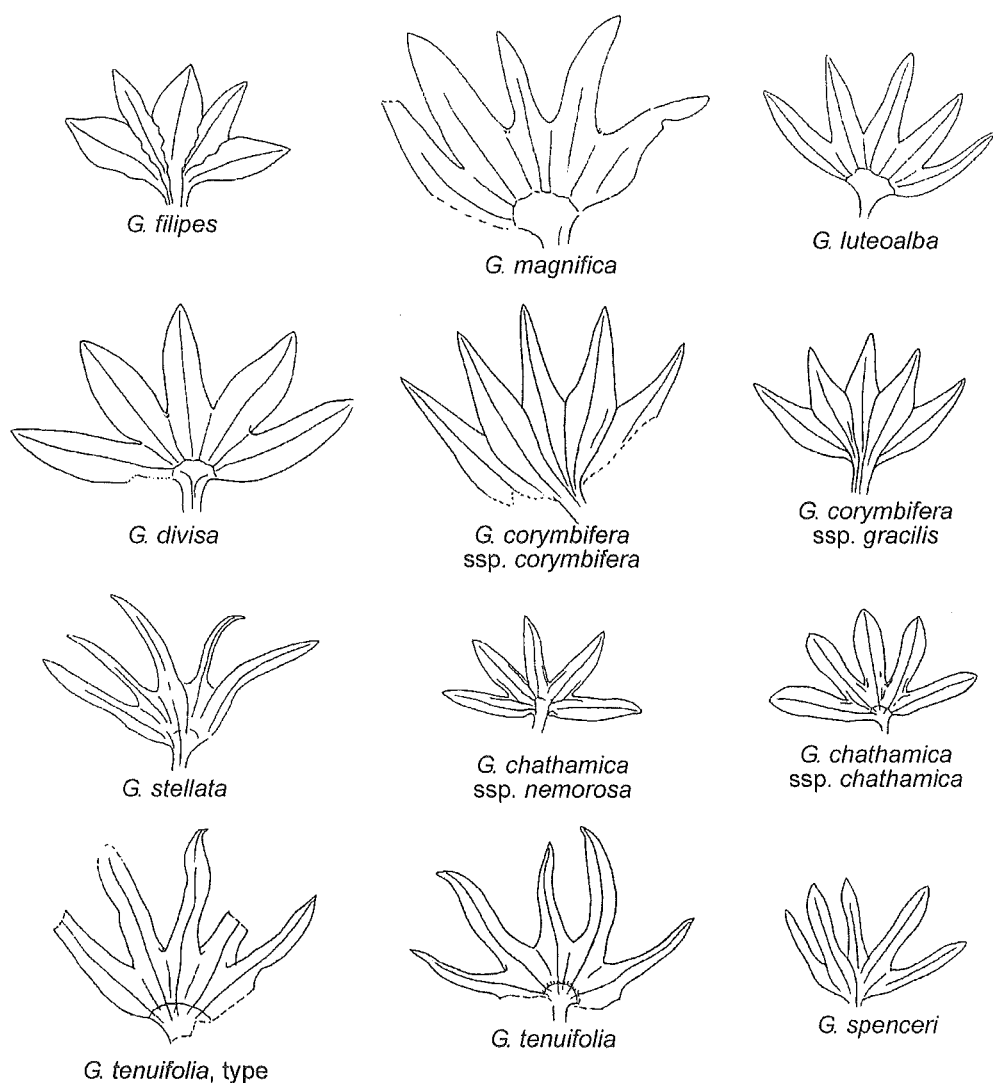


Fig. 5 Calyces of species in the *Gentianella divisa* and *G. spenceri* groups.

G. divisa group: *G. filipes*: D. Glenny 6816, Mt Mytton, CHR530490; *G. magnifica*: J. McLintock, Barefell, CHR 526300; *G. luteoalba*: G. Jane, Hope Range, CHR 516247; *G. divisa*: D. Glenny 7476, Lake Wapiti, CHR 560103; *G. corymbifera* ssp. *corymbifera*: D. Glenny 6903, Broken River, CHR 559461; *G. corymbifera* ssp. *gracilis*: P. N. Johnson 1423, Glenmore Tarns, CHR 518390. *G. spenceri* group: *G. stellata*: G. Jane, Hackett Valley, CHR 526439; *G. chathamica* ssp. *nemorosa*: A. P. Druce, Kaimanawa Range, CHR 112770; *G. chathamica* ssp. *chathamica*: D. Glenny 7152, Chatham Is., CHR 559759; *G. tenuifolia*: type, W. Townson, Lyell, WELT 4721; *G. tenuifolia*: C. J. Burrows, Ashley Gorge, CHR 520188; *G. spenceri*: D. Glenny 7363, Granity Pass, CHR 559989.

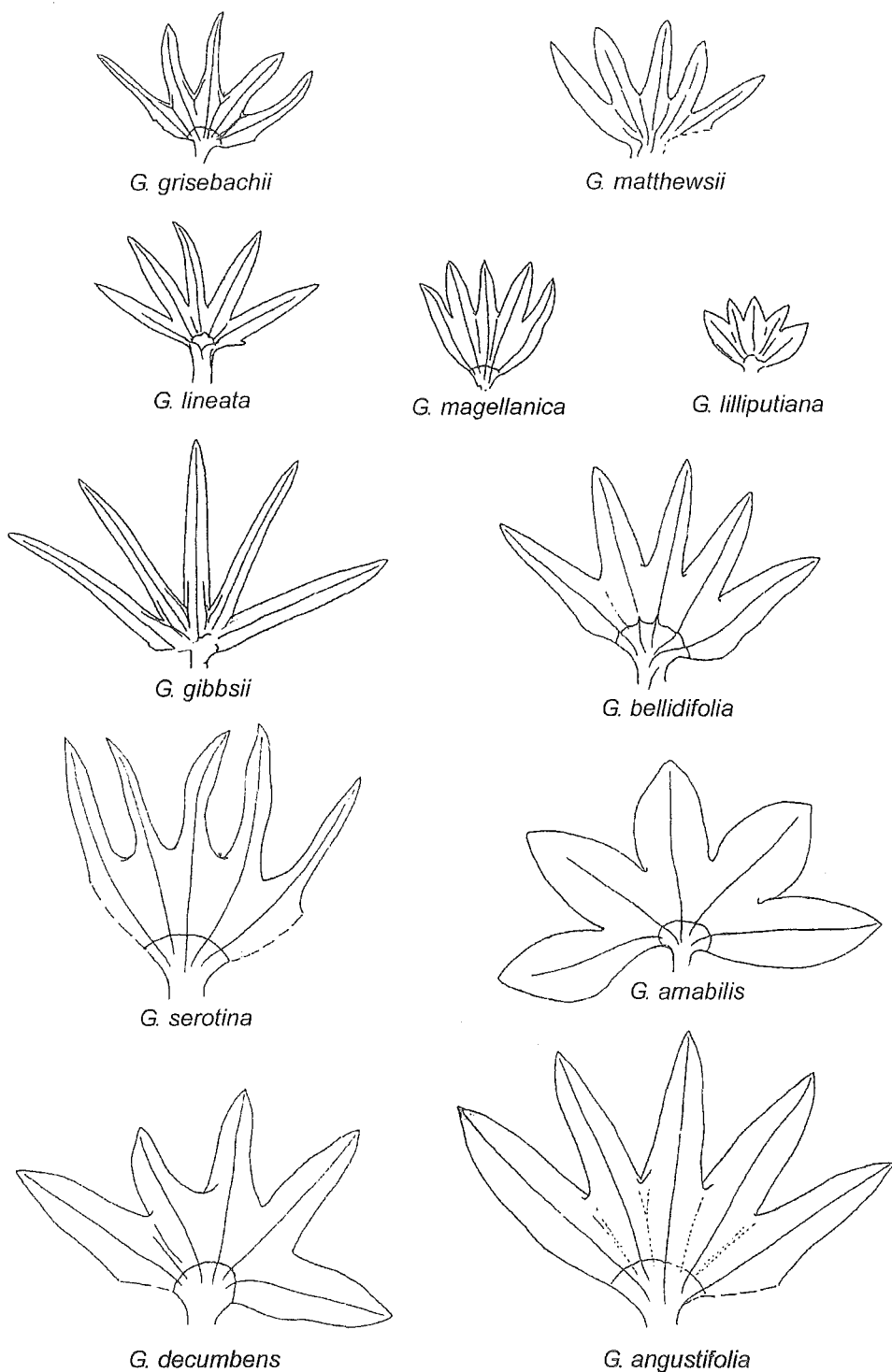


Fig. 6 Calyces of species in the *Gentianella grisebachii* group, *G. lilliputiana*, *G. magellanica*, and *G. bellidifolia* group.

G. grisebachii group: *G. grisebachii*: D. Glenny 6884, Rees V., CHR 559445; *G. matthewsii*: D. Glenny 6876, Lake Harris, CHR 530552; *G. lineata*: D. Glenny 7475, Lake Wapiti, CHR 560102; *G. gibbsii*: D. Glenny 6344, Mt Anglem, CHR 509867; *G. magellanica*: E. J. Godley 931, Chile, CHR 534629; *G. lilliputiana*: A. Mark, R. Allen, C. J. Webb, Lauder Ck, CHR 417292; *G. bellidifolia* group: *G. bellidifolia*: A. P. Druce, Mt Somers, CHR 395857; *G. serotina*: M. Sinclair, Rock and Pillar Ra., OTA 44772; *G. amabilis*: P. N. Johnson 1375, Old Man Range, CHR 511803; *G. decumbens*: A. P. Druce, Kakapo Peak, CHR 252186; *G. angustifolia*: A. P. Druce, Hoary Head, CHR 395841.

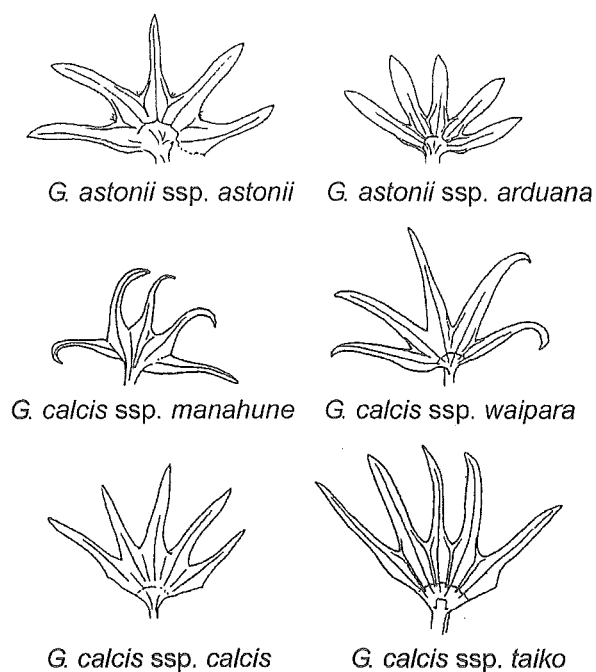


Fig. 7 Calyces of the *Gentianella astonii* group.

G. astonii ssp. *astonii*: D. Glenny 6414, Benmore, CHR 509942A; *G. astonii* ssp. *arduana*: D. Glenny 7488, Chalk Range, CHR 525472; *G. calcis* ssp. *manahune*: D. Glenny 8232, Manahune Station, CHR 560259; *G. calcis* ssp. *waipara*: D. Glenny 7456, Mt Brown, CHR 256518; *G. calcis* ssp. *calcis*: D. Glenny 8234, Awahokomo, CHR 560262; *G. calcis* ssp. *taiko*: D. Glenny 8233, Limestone Valley Rd, CHR 560260.

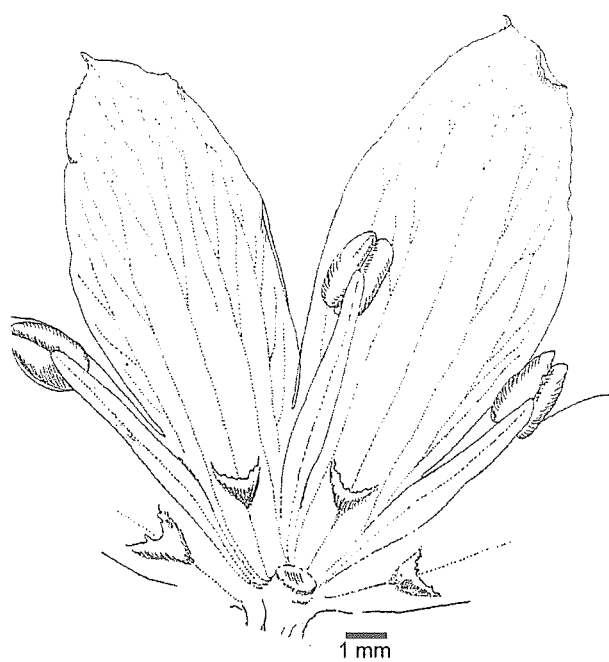


Fig. 8 Corolla of *Gentianella astonii* ssp. *astonii*. Ovary removed to show pocket-shaped nectaries with a toothed pocket margin. *D. Glenny 6416*, Benmore, CHR 509942A.

RESULTS

For the purposes of this revision, I placed all the New Zealand *Gentianella* species into eight species groups. The groups are: the *G. saxosa* group, *G. divisa* group, *G. montana* group, *G. spenceri* group, *G. grisebachii* group, *G. bellidifolia* group, *G. astonii* group, and *G. lilliputiana* group. A description of each group and membership of each group is provided in the Synopsis (Taxonomy Section). The relationships between these groups are in some cases clear, in other cases not. For instance, the *G. spenceri* and *G. grisebachii* groups are probably sibling groups, being made up mostly of relatively short but erect biennial species with coloured corollae. Both are probably most closely related to the taller and mostly polycarpic *G. montana* group. I am unable to say what the mutual relationships of the *G. divisa*, *G. saxosa*, and *G. bellidifolia* groups are, but there are similarities between the *G. montana* and *G. saxosa* groups in the leaf epidermal cells (Fig. 33) and the pollen surface pattern (Fig. 38) that suggests they have an immediate common ancestor. In the course of this revision, candidate taxa, mostly those recognised by A. P. Druce, were assigned to one of the species groups and assessed by comparison with the named species.

The *G. saxosa* group

This group comprises the four Subantarctic species (*G. concinna*, *G. cerina*, *G. antipoda*, and *G. antarctica*) and *G. saxosa* of Southland and Stewart Island. *G. cerina* var. *suberecta* was described by Kirk, and accepted as a variety by Cheeseman (1925) and Allan (1961) and needed assessment. Hooker and Kirk expressed doubts over the distinctness of *Gentiana cerina* and *G. concinna*. Hooker remarked to Kirk (reported in Kirk 1895) that they were impossible to separate specifically. Colin Meurk (pers. comm. 1995) expressed some doubt to me over the distinctness of these two. Thirdly, the population of *G. saxosa* first collected by Townson at Charleston and mentioned by Cheeseman (1925) had never been critically compared to Southland *G. saxosa* populations.

The Charleston gentian

The leaf shape map in Fig. 9 shows how different the Charleston gentian is in its leaf shape from Southland and Stewart Island populations of *G. saxosa*. It also shows how the leaves of specimens from southern Stewart Island are larger than those for the rest of the species' range. This difference is not reflected in any other characteristics of those populations.

The Charleston gentian differs from Southland and Stewart Island populations of *G. saxosa* in several other respects (Table 10). It has coloured corolla veins, and in this respect

is closer to the Subantarctic Island species of *Gentianella*. There is no doubt that the Charleston gentian is closer to *G. saxosa* than any other species in the group, but the number of differences between it and Southland and Stewart Island *G. saxosa* suggests a substantial period of isolation. I have chosen to describe it as a species on the basis of the the number of these differences.

Table 10 Comparison of the Charleston gentian (*Gentianella scopulorum*) and *G. saxosa*, allopatric species.

	<i>G. scopulorum</i>	<i>G. saxosa</i>
Flowering stem colour	crimson	purple-black
Leaf shape	orbicular	elliptic or narrowly elliptic
Pedicle length (mm)	1–16	10–67
Calyx lobes	plane	recurved
Calyx sinus hairs	absent, sparse or abundant	absent
Corolla length (mm)	9.5–14.8	13.7–15.7
Corolla colour	white with purple veins	white
Nectary distance from corolla base (mm)	0.7–1.2	2.5–3.7
Anther length (mm)	1.0–1.5	2.0–2.1

The Subantarctic gentians

There has been some difficulty reported in separating *G. concinna* and *G. cerina* in the field on the Auckland Islands, noted as early as Hooker’s remark to Kirk (reported in Kirk, 1895) that they were impossible to separate specifically. Colin Meurk (pers. comm. 1995) expressed some doubt over the distinctness of these two. Comparison of the pair indicates that there is no doubt as to their distinctness, as summarised in Table 11. There is no overlap in leaf length, leaf width, or calyx length. The two should be retained as species.

Table 11 Comparison of *Gentianella cerina* and *G. concinna*.

	<i>G. cerina</i>	<i>G. concinna</i>
Life cycle	polycarpic	monocarpic
Lateral flowering stem attitude	decumbent	erect
Leaf length (mm)	37–53	15–32
Leaf width (mm)	8.4–12.6	3.7–8.0
Pedicel diameter	1.2–1.3 mm, 0.7–1.0 mm dry	0.9–1.1 mm, 0.4–0.6 mm dry
Calyx length (mm)	9.3–12.2	6.0–8.8
Calyx lobe tip shape	pandurate and obtuse tipped	tapering and acute or obtuse tipped
Corolla length	8.4–11.8 mm, shorter than calyx	8.7–13 mm, longer than calyx

Kirk’s *G. cerina* var. *suberecta* was described in his 1895 revision of the New Zealand gentians, and the differences Kirk listed for his new variety from the type variety are listed in Table 12. Examination of specimens of *G. cerina* at CHR show both erect and decumbent forms, but they do not divide on habitat as suggested by Kirk. On the summit of Mt Eden, for instance, a plant of the decumbent and much branched type was collected by Godley (CHR 134051) while a plant of the erect and unbranched type was collected by Dawbin (CHR 368904). Similar variation can be seen in coastal collections. In this polycarpic species, specimens show great size variation, from those with a single flowering stem and only c. 10 flowers, to very large sprawling plants with many branches and more than 100 flowers. I was unable to see a difference in pedicel length between coastal and hill plants on herbarium sheets. Measurements of leaves, pedicels, and flowers from the type of *G. cerina* var. *suberecta* fall within the range of *G. cerina*. It is difficult to assess such a variety without making field observations, but my conclusion is that *G. cerina* is a phenotypically variable species and that what Kirk observed were differences due to habitat and plant age.

Table 12 *Gentiana cerina* var. *cerina* and var. *suberecta* as described by Kirk (1895).

	<i>Gentiana cerina</i> var. <i>cerina</i>	<i>Gentiana cerina</i> var. <i>suberecta</i>
Stem attitude	prostrate or trailing	decumbent, ascending or erect, 6–12" (15–30 mm) or more
Leaf shape	obovate or spatulate-oblong	spathulate-oblong
Leaf petiole	narrowed below	petiolate or rarely sessile by a broad base
Pedicels	flowers often sunken among leaves	short to long pedicels
Calyx lobes	slightly recurved	broadly oblong
Habitat	coastal rocks	hills to 1000 feet (300 m)

The type of *G. antarctica* var. *imbricata* consists of small plants similar to the small ones of those illustrated by Godley (1982). Kirk distinguishes it by the absence of warts (these are caused by a fungus, as pointed out by Allan 1961), coriaceous leaves with "strong marginal nerves" which refers to the recurved margin of *G. antarctica*, and larger flowers. A flower on the type is 8.5 mm long, within the range for the species. For these reasons, the variety is rejected.

Hooker's *G. concinna* var. *robusta* and *G. concinna* var. *elongata* were named from specimens from Campbell Island. Inspection of specimens at CHR from Campbell Island does not show any variation that needs taxonomic recognition. However, field observations are needed for greater certainty on this. I have not seen Hooker's types.

There is a trend from *G. saxosa* to *G. antipoda* in a number of characters that is summarised in Table 13. Life cycle shows a trend from polycarpic to monocarpic, leaf apex from rounded to acute, leaf margins from not thickened to thickened, pedicels from long to short, calyces from shallowly to deeply lobed, corolla sinus hairs from present to absent, corolla and anther from long to short, and ovule number from many to few.

Table 13 Characteristics of species within the *Gentianella saxosa* group.

	<i>G. saxosa</i>	<i>G. scopulorum</i>	<i>G. cerina</i>	<i>G. concinna</i>	<i>G. antarctica</i>	<i>G. antipoda</i>
Life-cycle	polycarpic	polycarpic	polycarpic	monocarpic	monocarpic	monocarpic
Leaf apex shape	rounded	rounded	rounded/retuse	rounded	acute to rounded	acute to rounded
Leaf margin thicker	no	no	yes	yes	yes	yes
Pedicel length (mm)	10–67	1–16	6.2–17.8	4.0–7.0(–11.5)	1.6–4.5	0.8–2.0
Depth of calyx lobing	c. 0.66	c. 0.65	0.80–0.84	0.81–0.91	0.72–0.92	0.84–0.88
Corolla sinus hairs	present	present	present/absent	present	sparse/absent	absent
Corolla length (mm)	13.7–15.8	9.5–14.8	8.4–11.8	8.7–13.0	9.5–14	5.4–10.5
Nectary distance (mm)	2.5–3.7	0.7–1.2	1.2–1.5	1.2–1.5	1.6–3.4	1.0–1.4
Anther length (mm)	2.0–2.1	1.0–1.5	0.9–1.7	1.2–1.8	1.0–1.2	0.75–1.0
Ovule number	30–44	16–30	13–37	13–40	7–27	3–9

The development of the monocarpic life cycle on the Subantarctic Islands is associated with a trend to smaller floral parts (ovule number, anther length, corolla length, pedicel length) with an extreme selfing syndrome seen in *G. antipoda*. Many of the characters listed here are probably correlated, but it is not unreasonable to suggest that *G. antarctica* and *G. antipoda* are sibling species and that they have their nearest related species in *G. concinna*, *G. cerina*, or their immediate ancestor, rather than *G. saxosa*.

Of the five species in the group, *G. saxosa* is the most distinct. It has large white flowers with long anthers, on long pedicels. The leaf margin is not thickened as it is in the Subantarctic species. The degree of calyx lobing is less than for the Subantarctic species. Some of these characteristics result from it being an outcrossing species in contrast to the Subantarctic species.

Although the monocarpic Subantarctic gentians have been described as annual, perhaps because Cheeseman (1906, 1925) and Allan (1961) used the term annual to mean monocarpic, Godley (1982) presents evidence that at least *G. antarctica* is biennial. *G. antipoda* and *G. concinna* are even more robust and often have more flowering stems than

G. antarctica, and so are probably also biennial.

A conspicuous feature of both *G. saxosa* and *G. antarctica* is the distance from the base of the corolla to the nectaries, so that the nectaries are positioned very near the point of insertion of the filaments on the corolla wall, much further from the base of the corolla than in the other species.

Adams (1995) suggested that *Gentianella demissa* from Tasmania might be related to the New Zealand Subantarctic Island gentians. A herbarium specimen of *G. demissa* was compared to the *G. saxosa* group of species. The species (Adams 1996, fig 47M) has at least a superficial resemblance to *G. concinna* the monocarpic species on the Auckland Islands. The specimen was scored for those characters that define the *G. saxosa* group of some of its members, particularly *G. concinna*. The results are summarised in Table 14.

Table 14 Comparison of *Gentianella demissa* and gentians of the *G. saxosa* group.

	<i>G. demissa</i>	<i>G. saxosa</i> group
Pollen grains	striate-reticulate	striate
Epidermal leaf cells	zigzagged	quadrate
Life cycle	monocarpic	monocarpic (4 species), polycarpic (2 species)
Leaf apex	rounded	rounded in most species
Leaf margin	not thickened	thickened in Subantarctic Island species
Leaf midvein	projecting	not projecting in some species
Pedicel length	short, 0.5–6.5 mm	short, (0.8–)2–7(–18) except in <i>G. saxosa</i>
Calyx lobe shape	widest at their base	wider toward the apex in some species
Calyx lobe apex	acute	rounded (1 species), acute (5 species)
Calyx lobe depth	×0.71 the calyx length	×0.72–0.92 in Subantarctic Island species
Anther length	1.5–1.9 mm	0.75–1.7 mm in Subantarctic Island species
Ovule number	40–45 per ovary	3–44 per ovary

G. demissa does not share the most constant character states of the *G. saxosa* group (striate pollen grain pattern, non-zig-zag leaf epidermal cell shape). Character states that are in common (e.g., short pedicel length) are ones where homoplasy might easily arise. It appears that *G. demissa* does not have its closest relatives on the New Zealand Subantarctic Islands.

The classification of the group stays unchanged except for the addition of a new

species *G. scopulorum* (the Charleston gentian) and *G. cerina* var. *suberecta* is not recognised (Table 15).

Table 15 Concordance of names in the New Zealand *Gentianella*. *G^a*. = *Gentiana*.

Kirk 1895	Cheeseman 1925	Allan 1961	this revision
<i>G. SAXOSA GROUP</i>			
<i>G. saxosa</i>	<i>G^a. saxosa</i>	<i>G^a. saxosa</i>	<i>G. saxosa</i>
-	-	-	<i>G. scopulorum</i> (Charleston gentian)
<i>G^a. cerina</i>	<i>G^a. cerina</i>	<i>G^a. cerina</i>	<i>G. cerina</i>
<i>G^a. cerina</i> forma <i>suberecta</i>	<i>G^a. cerina</i> var. <i>suberecta</i>	<i>G^a. cerina</i> var. <i>suberecta</i>	<i>G. cerina</i>
<i>G^a. cerina</i> forma <i>concinna</i>	<i>G^a. concinna</i>	<i>G^a. concinna</i>	<i>G. concinna</i>
<i>G^a. antarctica</i>	<i>G^a. antarctica</i>	<i>G^a. antarctica</i>	<i>G. antarctica</i>
<i>G^a. antipoda</i>	<i>G^a. antipoda</i>	<i>G^a. antipoda</i>	<i>G. antipoda</i>
<i>G. DIVISA GROUP</i>			
<i>G^a. corymbifera</i>	<i>G^a. corymbifera</i>	<i>G^a. corymbifera</i>	<i>G. corymbifera</i> subsp. <i>corymbifera</i>
-	-	-	<i>G. corymbifera</i> subsp. <i>gracilis</i> ("narrow-leaved form")
<i>G^a. bellidifolia</i> var. <i>divisa</i>	<i>G^a. divisa</i>	<i>G^a. divisa</i>	<i>G. divisa</i>
<i>G^a. bellidifolia</i> var. <i>magnifica</i>	-	<i>G^a. divisa</i> var. <i>magnifica</i>	<i>G. magnifica</i> (<i>G^a</i> . "Barefell")
-	-	-	<i>G. luteoalba</i> (<i>G^a</i> . "Lookout")
<i>G^a. bellidifolia</i> var. <i>vacillata</i>	<i>G^a. divisa</i>	<i>G^a. divisa</i>	<i>G. corymbifera</i>
<i>G. MONTANA GROUP</i>			
<i>G^a. montana</i> in part	<i>G^a. montana</i>	<i>G^a. montana</i>	<i>G. montana</i> subsp. <i>montana</i>
-	<i>G^a. montana</i> var. <i>stolonifera</i>	<i>G^a. montana</i> var. <i>stolonifera</i>	<i>G. montana</i> var. <i>stolonifera</i>

Kirk 1895	Cheeseman 1925	Allan 1961	this revision
-	<i>G^a. tereticaulis</i>	<i>G^a. tereticaulis</i>	<i>G. montana</i> subsp. <i>montana</i>
<i>G^a. montana</i> in part	<i>G^a. patula</i> in part	<i>G^a. patula</i> in part	<i>G. montana</i> subsp. <i>ionostigma</i>
<i>G^a. bellidifolia</i> var. <i>patula</i>	<i>G^a. patula</i> in part	<i>G^a. patula</i> in part	<i>G. patula</i> (Cobb gentian)
-	<i>G^a. townsonii</i>	<i>G^a. townsonii</i>	<i>G. montana</i> var. <i>stolonifera</i>
-	<i>G^a. vernicosa</i>	<i>G^a. vernicosa</i>	<i>G. vernicosa</i>
-	<i>G^a. gracilifolia</i>	<i>G^a. gracilifolia</i>	<i>G. vernicosa</i>
-	-	-	<i>G. impressinervia</i> (<i>G^a. "Paparoa"</i>)
<i>G. SPENCERI</i> GROUP			
<i>G^a. spenceri</i>	<i>G^a. spenceri</i>	<i>G^a. spenceri</i>	<i>G. spenceri</i>
-	<i>G^a. tenuifolia</i>	<i>G^a. tenuifolia</i>	<i>G. tenuifolia</i>
<i>G^a. pleurogynoides</i> var. <i>umbellata</i> in part	-	-	<i>G. stellata</i> (<i>G^a. "stellar"</i>)
<i>G^a. pleurogynoides</i> var. <i>umbellata</i> in part	<i>G^a. chathamica</i>	<i>G^a. chathamica</i>	<i>G. chathamica</i> subsp. <i>chathamica</i>
-	-	-	<i>G. chathamica</i> subsp. <i>nemorosa</i> (<i>G^a. "volcanic plateau"</i>)
<i>G. GRISEBACHII</i> GROUP			
<i>G^a. montana</i> forma <i>grisebachii</i>	<i>G^a. grisebachii</i>	<i>G^a. grisebachii</i>	<i>G. grisebachii</i>
-	<i>G^a. grisebachii</i> var. <i>matthewsii</i>	<i>G^a. matthewsii</i>	<i>G. grisebachii</i>
<i>G^a. lineata</i>	<i>G^a. lineata</i>	<i>G^a. lineata</i>	<i>G. lineata</i>
-	<i>G^a. gibbsii</i>	<i>G^a. gibbsii</i>	<i>G. gibbsii</i>
<i>G. BELLIDIFOLIA</i> GROUP			
<i>G^a. bellidifolia</i>	<i>G^a. bellidifolia</i>	<i>G^a. bellidifolia</i>	<i>G. bellidifolia</i>

Kirk 1895	Cheeseman 1925	Allan 1961	this revision
-	<i>G^a. bellidifolia</i> var. <i>australis</i>	<i>G^a. bellidifolia</i> var. <i>australis</i>	<i>G. bellidifolia</i>
<i>G^a. bellidifolia</i> var. <i>pulchella</i>	-	<i>G^a. bellidifolia</i> var. <i>pulchella</i>	-
-	-	<i>G^a. amabilis</i>	<i>G. amabilis</i>
-	<i>G^a. serotina</i>	<i>G^a. serotina</i>	<i>G. serotina</i>
-	-	-	<i>G. angustifolia</i> (<i>G^a. "long narrow leaves"</i>)
-	-	-	<i>G. decumbens</i> (<i>G^a. "decumbent"</i>)
<i>G. ASTONII</i> GROUP			
-	<i>G^a. astonii</i>	<i>G^a. astonii</i>	<i>G. astonii</i> subsp. <i>astonii</i>
-	-	<i>G^a. astonii</i> in part	<i>G. astonii</i> subsp. <i>arduana</i> (<i>G^a. "Chalk"</i> and <i>G^a. "Ward"</i>)
-	-	<i>G^a. astonii</i> in part	<i>G. calcis</i> subsp. <i>waipara</i> (<i>G^a. "Brown"</i>)
-	-	-	<i>G. calcis</i> subsp. <i>manahune</i> (<i>G^a. "Manahune"</i>)
-	-	-	<i>G. calcis</i> subsp. <i>taiko</i> (<i>G^a. "Pareora"</i>)
-	-	<i>G^a. astonii</i> in part	<i>G. calcis</i> subsp. <i>calcis</i> (<i>G^a. "Awahokomo"</i>)

The *G. divisa* group

This group has three named species, *G. filipes*, *G. divisa* and *G. corymbifera* and one infraspecific taxon, *G. divisa* var. *magnifica*.

Allan did not recognise *G. bellidifolia* var. *vacillata* Kirk and discussed it under *G. divisa*. In addition to these four taxa, A. P. Druce recognised two entities which, in my opinion, belong in this group of species. Firstly, a gentian from the Lookout Range in Nelson, *G. "Lookout"*. The Lookout gentian was first noted by Bell (1973), who referred to it as *Gentianella* sp. (WELTU 7962) from the Lookout Range. It occurs 195 km to the north of the northern limit of *G. divisa* at the Torlesse Range, and 78 km to the north-east of the Barefell gentian. Secondly, Druce (1992a) listed an unnamed taxon, *Gentiana* "Skeleton"

from the Eyre Mountains, Garvie Mountains (Skeleton Lake) and Kea Basin. These two candidate taxa needed to be compared to *G. divisa*.

Gentiana bellidifolia var. *vacillata* has two syntypes. One is a Kirk specimen from Mount Earnslaw which is missing but was probably a collection of *G. divisa*. The other is a collection of J. B. Armstrong's from "Canterbury Plains, 1000 ft", WELT 4716, which appears to have been cited by Kirk as "Canterbury Alps" in his protologue. This specimen is probably *G. corymbifera*, as a leaf on the specimen has a petiole 6.3 mm wide, wider than seen in most *G. divisa* specimens, and is consistent with the specimen being from a lower altitude (1000 ft). Since the Earnslaw syntype is missing, the Canterbury Alps syntype is nominated here as the lectotype. *G. bellidifolia* var. *vacillata* as a result is a synonym of *G. corymbifera*, a change from the synonymy of Cheeseman (1925, p. 733) and Allan (1961, p. 773).

Gentiana pleurogynoides var. *rigida* Kirk has six syntypes and are all specimens of *G. corymbifera*. They are collections of Heinrich von Haast from "above Jollies Pass" (WELT 47817), "Dr von Haast" from [the] Rakaia [Valley] (WELT 47814), Kirk's from Amuri (WELT 47820), Petrie's from Otago (WELT 47774), Kirk's from "Canterbury Alps" (WELT 47773), and a collection without locality or collector's name (WELT 43508). I have chosen the Jollies Pass specimen as the lectotype. None of the collections are *G. serotina* as suggested in Allan (1961, p. 773) but a determination "cf. *serotina* J.A.H[ay] 9/7/51" on the Amuri and Rakaia specimens is probably the origin of this comment.

G. divisa and *G. corymbifera* are sibling species that share bienniality and a stout terminal flowering stem giving rise to a dense corymb of white flowers (Table 16). *G. filipes* is a small annual species and is not so obviously a member of this group of species. I believe it belongs here because it is monocarpic, it has leaf and stem tissues that are either untinted or tinted purple-black (in common with some *G. corymbifera*), it has short broadly triangular calyx lobes like those of *G. divisa* and *G. corymbifera*, and these have ridges formed by recurved margins, a feature of *G. divisa*. *G. filipes* and *G. divisa* commonly have female flowers. The ridged calyx lobe margins and the rugose outer calyx surface of *G. filipes* and *G. divisa* convinces me that they are sibling species.

Table 16 Differences between *Gentianella corymbifera* s. l. and *G. divisa*, two widespread species that overlap in their distribution but are rarely found together.

	<i>G. corymbifera</i> s. l.	<i>G. divisa</i>
Plant height (mm)	60–470	40–200
Flower stem structure	not condensed, stem always visible	usually condensed, stem often not visible among flowers and stem leaves
Stem diameter (mm)	4.2–10.1	1.7–5.0
Leaf length (mm)	(15–)40–168	16–65
Petiole width (mm)	(1.5–)3.0–12.0(–18.5)	2.8–8.0
Female flowers	rare	common
Calyx lobe surface	smooth	rugose
Keels on calyx below lobe margins	not conspicuous	conspicuous

Variation in Gentianella corymbifera

Wilson (1978) noticed that *Gentianella corymbifera* at Mount Cook had two forms, a "broad-leaved" form of subalpine and alpine habitats, and a "narrow-leaved" form of montane river flats and feet of spurs. Wilson's narrow-leaved form has often been identified as *G. serotina*, but has terminal flowering stems unlike *G. serotina*. Nelson plants of *G. corymbifera* are more branched than those to the south, with particularly distinct plants occurring at Granity Pass near Mt Owen. These plants are difficult to assign to *G. corymbifera* rather than *G. montana* which is also common in the Nelson mountains and is itself a very variable species. To analyse the variation, specimens were assigned to one of three types: the narrow-leaved form, the normal *G. corymbifera* corresponding to the type from St James Station, and the Nelson form. Marlborough plants were left out of the comparison because I was unsure whether to group them with the Nelson plants or Canterbury plants. The three forms were compared using 11 characters that characterised their important differences (Table 17).

Table 17 Analysis of variation within *Gentianella corymbifera*. Sample minimum, mean, and maximum are given.

	Narrow-leaved form	<i>t</i>	<i>G. corymbifera</i> s. s.	<i>t</i>	Nelson form
Plant height (mm)	90-210-370 (<i>n</i> = 19)	0.6 -	60-290-640 (<i>n</i> = 16)	0.7 -	200-420-500 (<i>n</i> = 10)
Leaf length (mm)	41-79-127 (<i>n</i> = 11)	0.6 -	41-72.4-168 (<i>n</i> = 24)	0.05 -	41-75-109 (<i>n</i> = 13)
Leaf width (mm)	5.0-8.4-11.5 (<i>n</i> = 11)	3.4 **	6.5-16.1-31 (<i>n</i> = 22)	0.1 -	11.0-16.4-22.5 (<i>n</i> = 13)
Petiole width (mm)	1.5-3.7-5.2 (<i>n</i> = 11)	4.2 ***	4.0-7.6-18.5 (<i>n</i> = 15)	0.4 -	4.2-7.05-12.5 (<i>n</i> = 11)
Flowering stem diameter (mm)	1.2-3.1-6.9 (<i>n</i> = 7)	12 ***	4.2-6.0-10.5 (<i>n</i> = 21)	4 ***	2.2-4.8-6.5 (<i>n</i> = 9)
Flower number	5-27-98 (<i>n</i> = 12)	0.1 -	7-55-166 (<i>n</i> = 12)	0 -	7-55-110 (<i>n</i> = 7)
Calyx length (mm)	5.2-6.5-8.0 (<i>n</i> = 8)	11 ***	6.8-9.5-14.0 (<i>n</i> = 19)	0.5 -	7.1-9.1-13.0 (<i>n</i> = 7)
Largest calyx lobe width (mm)	1.7-2.1-2.6 (<i>n</i> = 7)	38 ***	2.5-3.0-3.5 (<i>n</i> = 14)	4.8 ***	2.7-3.2-3.9 (<i>n</i> = 6)
Corolla length (mm)	11.0-13.4-14.6 (<i>n</i> = 6)	2.8 *	14.0-17.7-21.2 (<i>n</i> = 14)	0.8 -	11.5-15.8-25.7 (<i>n</i> = 7)
Filament width (mm)	0.75-0.93-1.35 (<i>n</i> = 8)	44 ***	1.0-1.5-1.6 (<i>n</i> = 4)	11 ***	(0.6-) 1.1-1.24-1.4 (<i>n</i> = 7)
Anther length (mm)	2.0-2.3-2.7 (<i>n</i> = 6)	5.2 ***	1.6-2.2-2.6 (<i>n</i> = 17)	19 ***	2.2-2.9-3.6 (<i>n</i> = 7)

The sample means of the narrow-leaved form differ from *G. corymbifera* s. s. in the following respects: the plants are shorter, the terminal flowering stem is narrower, there are fewer flowers per plant, the leaf and petiole widths are narrower by half, the calyx is shorter and the lobes are narrower, and the filaments are narrower. Despite these significant differences in means, the ranges overlap between the two forms for all characters.

However, the number of differences suggest that the narrow-leaved form is a distinct taxon. Its geographic range overlaps that of *G. corymbifera* s. s. between Broken River basin and Otago. In the intermontane basins of the Waimakariri, Rakaia, Ashburton, Rangitata, and Waitaki rivers, the narrow leaved form is most often found on moraine and outwash surfaces in the basin floors, while *G. corymbifera* s. s. is mostly alpine on the mountains surrounding these basins. However, in Otago, the narrow leaved form is found in

a greater variety of habitats, on hillslopes and in stream gullies, while *G. corymbifera* s. s. is very uncommon and mostly alpine. In Canterbury, where the two forms are equally abundant, the two are separated by altitude. For instance, at Freehold Creek above the western shores of Lake Ohau, the narrow-leaved form is common on lateral moraines near the lake but extends some way up the slopes of the Ohau Range behind. On top of the range, *G. corymbifera* s. s. is common on peat soils in alpine bogs, and is less common on the upper slopes of the range. It is difficult to say whether the two forms ever meet at mid-slope on the range, as the species is virtually absent at those intermediate altitudes. It is possible to assign about 90% of specimens to the broad-leaved or narrow-leaved form, using the key devised. In the other 10% of specimens, characters were inconsistent (e.g., stem diameter indicated the narrow-leaved form, but filament width indicated the broad-leaved type). Fig. 10 shows leaf shapes of both types from which it can be seen that there is some overlap, but in most cases the two can be distinguished on leaf shape and size alone. I conclude that the narrow-leaved form should be distinguished as a subspecies.

The Nelson form differs significantly from *G. corymbifera* s. s. in fewer respects than does the narrow-leaved form. The plants are taller, and the anthers longer. Three additional characters that noticeably differ are the length of the caudex, the branching of the caudex and the occasionally polycarpic life cycle. The Nelson form has a caudex of 85–110–130 mm (n = 6) that branched in 2 of 6 cases, while *G. corymbifera* s. s. and the narrow-leaved form both had caudices too short to measure or not exceeding 15 mm, and branched in only 2 of 14 cases. The Nelson form is occasionally polycarpic (e.g., *D. Glenny* 7719, Culliford Hill, CHR 525492), a state seen only once in *G. corymbifera* s. s. outside of Nelson (*D. Glenny* 6920, Westland, Trent River, CHR 559477).

Nelson populations of *G. corymbifera* are geographically separated from Canterbury populations of *G. corymbifera* s. s. (Fig. 11). Canterbury *G. corymbifera* has its north-western limit at the head of the Clarence Valley, and is absent from Nelson Lakes National Park and the Raglan Range. Sixty-five kilometres to the north, the main Nelson population has its southern limit at the Marino Mountains, and extends northwards to the Anatoki Range, and as far west as the Garibaldi Range. Seventy kilometres to the north east it is present on the Gordon Range and Ben Nevis. In Marlborough, *G. corymbifera* is common on Molesworth station south of the Awatere River but on the north side of the Awatere River it has been collected only at Altimarlock and Wards Peak. It is then found on Mt Stokes, 75 km to the north. Altimarlock and Mt Stokes plants are very large and resemble plants in the Nelson mountains. Specimens from the Marino Mountains have a distinctly narrow leaf shape (Fig. 10, Granity Pass and Poverty Basin) which resembles that of *G.*

montana. This leaf shape, taken with the long caudex with its leaf scar pattern, and the often many branched caudex, make it difficult to distinguish from *G. montana* except in autumn when most *G. corymbifera* plants are dying, at which time *G. montana* plants remain green. Possibly, in this area, *G. corymbifera* has hybridised with *G. montana*. The evidence indicates that while there is a geographical variant in Nelson and Marlborough, it has insufficient differences to justify its recognition as a subspecies.

Further variation in *G. corymbifera* in North Canterbury can be seen between valley floor populations and alpine populations. Valley floor plants usually have only one flowering stem without laterals, are smaller leaved and generally less robust. Alpine plants usually have laterals and can be exceptionally large-leaved (viz. the leaf of a plant from No Mans Creek in Fig. 10). These differences mirror those seen in South Canterbury between *G. corymbifera* s. s. and the narrow leaved form. In both cases it is likely that separation by continuous forest on the mountain slopes allowed them to become distinct, but the differences are less marked in North Canterbury than in South Canterbury and Otago.

Gentiana divisa var. *magnifica* and the Barefell gentian

Gentiana bellidifolia var. *magnifica* Kirk was described from a specimen collected on Mt Captain in the Hanmer Range. Allan (1961) transferred the variety to *G. divisa* var. *magnifica*, as it has a stout terminal flowering stem which *G. bellidifolia* never has. A similar gentian was more recently found on Barefell on the Rachel Range 50 km to the north of Mt Captain. Both Barefell and Mt Captain have fine black argillite screes, and it was likely that the Barefell gentian was *G. divisa* var. *magnifica*. Fieldwork on Mt Captain in February 1999 failed to locate any plants resembling *G. divisa* var. *magnifica*. Black screes are also visible on Miromiro, a peak to the west of Mt Captain, where a collection of this gentian was made by Petrie in 1923 (CANU 2931). Two visits to Barefell failed to coincide with a mass flowering, and only two flowering plants from that locality have been available to compare to the Mt Captain and Miromiro specimens. One of the two Barefell specimens (*D. Glenny* 7451, CHR 529216) is an exceptionally large plant, having 238 flowers (the other three have between 45 and 86 flowers), the tap root is particularly robust (13 mm diameter), the stem diameter (7.3 mm) matches large specimens of *G. corymbifera*, and the seeds are 1.5 mm diameter, well above the seed diameter measured from any other New Zealand gentian (on average 1.0 mm diameter). The seeds in the type of var. *magnifica* were only 1.1 mm diameter (not rehydrated). The very large Barefell plant called into question whether the Barefell population could be assigned to *G. divisa* var. *magnifica*. The affinity of *G. divisa* var. *magnifica* and the Barefell gentian to *G. corymbifera* or *G. divisa*

was unclear. The relationships among *G. divisa* var. *magnifica* and the robust Barefell specimen, *G. divisa*, and *G. corymbifera* were unclear and it was necessary to do a principal components analysis.

Principal components analysis

A PCA of the four named taxa and three candidate taxa of the *G. divisa* group was done using 12 characters: plant height, flowering stem diameter, leaf length, leaf width, petiole width, flower number, calyx length, calyx lobe length, calyx lobe width, corolla length, distance of the nectary from the corolla base, filament width, anther length, and the number of ovules per ovary. The taxa sampled were *G. divisa* (8 samples), *G. filipes* (4 samples), *G. "Lookout"* (3 samples), *G. "Barefell"* (2 samples), *G. divisa* var. *magnifica* (the type and Petrie's Miromiro specimen), *G. corymbifera* s. s. (18 specimens) and *G. corymbifera* "narrow leaved form" (8 samples). To reduce scatter the values used were often means taken from more than one measurement from the same plant. A problem in this data set was missing values in 13 of the 574 cells. To overcome this, cells were filled using averages from other samples of the same taxon. In the case of *G. divisa* var. *magnifica*, the stem diameter was estimated from the root diameter and multiplied to give a fresh diameter using a conversion factor of $\times 1.25$ derived from other specimens where both states were known. This estimation method seemed preferable to omitting the character as stem diameter is an important character for separating *G. corymbifera* s. s. from its narrow leaved form, and from *G. divisa*. In the results stem diameter is well correlated with plant height.

Principal components I and II explained 44% and 24% of the variance respectively (Fig. 12), while component III explained 11% of the variance but was unhelpful in separating the groups and is not presented. Vegetative characters clustered closely, but floral characters were scattered, and ovule number was independent of these (Fig. 13). Most species and candidate taxa form discrete groups with little overlap, but the distances between some groups is small. However, individual groups are often not particularly distinct from good separation of *G. filipes* and *G. "Lookout"* from *G. divisa* on components I and II and indicates that *G. "Lookout"* is intermediate between *G. filipes* and *G. divisa*.

G. divisa and *G. corymbifera* do not overlap in their component I and II scores but are not well separated. A specimen that lies between the two groups is *G. divisa* (*G. Spearpoint*, Hitchin Range, South Westland, CHR 518969). This specimen reflects the difficulty in distinguishing *G. divisa* and *G. corymbifera* in the southern South Island.

Specimens of the narrow-leaved form of *G. corymbifera* differ from the broad leaved form of *G. corymbifera* in their component I scores. These correspond to lower

values for plant height, stem diameter, corolla length, flower number, anther length, petiole width and leaf width. The result confirms the distinctness of this taxon. However, the analysis gives little support for recognition of Nelson and Marlborough plants as a subspecies in *G. corymbifera*. Specimens of *G. corymbifera* with high component I scores were large plants from No Mans Creek and Altamarlock in Marlborough, and Mytton Creek in Nelson. Two Marlborough and Nelson specimens (from Mt Fyffe and Culliford Basin respectively) are mixed with specimens from Canterbury populations.

G. divisa var. *magnifica* and the Barefell gentian are distinct from *G. divisa* and *G. corymbifera*. The large size of the specimen *D. Glenny* 7451 from Barefell is apparent. Its component I score matches those of the largest specimens of *G. corymbifera*, but it has very low values in component II that reflect its very large calyx and corolla, the large number of flowers, and the low number of ovules. However, it shows in an extreme form a trend that is evident in the two specimens of *G. divisa* var. *magnifica* and the other Barefell specimen. Their component I and II scores together place them nearest to *G. divisa*. The smaller Barefell specimen is close to the two *G. divisa* var. *magnifica* specimens in its component I and II values, and justifies regarding the Hanmer Range and Rachel Range specimens as a single taxon. The PCA result suggests that *G. divisa* var. *magnifica* has its origin in *G. divisa*. The differences between *G. divisa* var. *magnifica* and *G. divisa* (Table 18) justify recognition of *G. divisa* var. *magnifica* as a species.

Table 18 Differences between *Gentianella magnifica* and *G. divisa*, allopatric sibling species.

	<i>G. magnifica</i>	<i>G. divisa</i>
Root diameter (mm)	8–13	2–6
Stem diameter (mm)	5.7–7.3	1.7–5.0
Leaf shape	narrowly elliptic	elliptic to obovate
Leaf apex shape	acute	rounded
Number of flowering stems per plant	ca. 10–40	ca. 5–10
Number of flowers per plant	45–220(–256)	11–60
Calyx length (mm)	12.3–20.0	8.5–11.0
Corolla length (mm)	17.2–24.5	13.5–18.6
Ovules per ovary	9–23(–37)	29–56(–76)
Seed diameter (mm)	1.1–1.5	c. 0.75

The Lookout gentian

The Lookout gentian is certainly closer to *G. divisa* than to any other species in the *G. divisa* group. Both have a terminal, compact inflorescence that hides the flowering stem, an abundant rosette of leaves at flowering time, and short rosette leaves with a short long petiole. The Lookout gentian is distinct from *G. divisa* in having narrower leaves that do not widen at midleaf as they do in *G. divisa*; a leaf epidermal cell pattern that is less zig-zagged than that of *G. divisa* (Fig. 34) and has thicker porose cell walls, and a shorter calyx. The corolla colour is a pale yellow, whereas it is always white in *G. divisa*, and the filaments are narrower. The capsules are smaller and the number of ovules fewer (Table 19). These differences are sufficient to justify recognition of the Lookout gentian as a species.

Table 19 Differences between the Lookout gentian (*Gentianella luteoalba*) and *G. divisa*, allopatric species.

	<i>G. luteoalba</i>	<i>G. divisa</i>
Leaf width (mm)	4.2–5.2	7.5–21
Leaf shape	lingulate	elliptic, obovate or narrowly obovate
Calyx length (mm)	6.7–8.4	8.5–11
Filament width (mm)	0.6–0.8	0.9–2.4
Ovules per ovary	9–20	29–56(–76)
Capsule length (mm)	5.6–7.5	15–17

The Skeleton Lakes gentian

Druce (1992a) gave the following diagnosis of *G. "Skeleton"*: "aff. *G. divisa* but plants more slender, 4–15 cm tall; basal lvs forming a dense rosette up to 7 cm diameter; stems numerous from near base, most branching; inflorescence produced well above lvs; calyx lobes subacute, sinus narrow; corolla c. 1 cm diameter". The measurements given in this description fall within those of *G. divisa* (e.g., in Canterbury *G. divisa* is 50–170 mm tall). *G. divisa* at Kea Basin on Mt Earnslaw does not differ in its appearance in the field from *G. divisa* at Gertrude Saddle in Fiordland. Specimens of *G. divisa* from Kea Basin have a blue stigma but so do plants of *G. divisa* from other Otago localities (e.g., *D. Glenny* 6874, Harris Saddle, CHR 559435; *D. Glenny* 8648, Fohn Saddle, CHR 524692; and *B. Brown*, Gillespies Pass, CHR 526443). This stigma colour difference was not a feature of *G. "Skeleton"* mentioned by Druce, and is insufficient to justify subspecific rank. This entity is treated as

part of *G. divisa*.

The classification of the *G. divisa* group adopted here differs from that of Allan (1961) by the raising of his *G. divisa* var. *magnifica* to species rank, by the addition of a new species related to *G. divisa* from the Lookout Range (*G. luteoalba*), and by the creation of a new subspecies within *G. corymbifera* (subsp. *gracilis*) — Table 15.

The *G. montana* group

Among the species recognised by Allan (1961) six belong to this group: *Gentiana montana*, *G. vernicosa*, *G. gracilifolia*, *G. patula*, *G. tereticaulis*, and *G. townsonii*. A number of problems with the circumscription of these species were evident. The identity of *G. patula* has never been established, as Kirk provided two syntypes and the name has not been lectotypified. Kirk's original description of it as a variety of *G. bellidifolia* suggests *G. patula* would be related to *G. bellidifolia*, but this is not necessarily the case, as he also considered *G. divisa* to be a variety of *G. bellidifolia*. Druce (1975) suggested that *Gentiana vernicosa* and *G. gracilifolia* were not distinct.

A relationship of *G. tereticaulis* to *G. tenuifolia* and *G. corymbifera* was suggested by Cheeseman (1925) and repeated in Allan (1961), the justification being that *G. tereticaulis* was "annual". It is evident from the type of *G. tereticaulis* that it is close to *G. montana*, but its distinctness from *G. montana* needed examination in the field, particularly since the monocarpic/polycarpic distinction was involved. That *G. townsonii* belonged to the *G. montana* group was also evident at the outset of this revision, but its status in relation to *G. montana* was unclear. Also, the distinctness of North Island populations of what had been determined variously as *G. montana* or *G. patula* needed assessment.

In addition to these named species, three candidate taxa needed assessment, *Gentianella* "Paparoa", and two other taxa whose affinities were unclear, *G. "Cobb"*, and a gentian collected from a South Westland pakihi by Peter Wardle which I called *G. "Gault"*.

Gentianella montana

While Cook's ship Resolution was moored at Cascade Cove, Anders Sparrman, the botanist of the expedition, climbed with William Pickersgill above Cascade Cove to collect (Begg & Begg 1966, pp. 42, 179). This is the only occasion while the Resolution was in Dusky Sound that collections were made above the treeline. The type of *G. montana* is probably from the tussock zone above treeline in the Mount Sparrman area. The lectotype chosen by Adams (1995, fig. 9) is a single flowering stem with several flowers at its apex. Only limited information can be gained from the lectotype as no rosette leaves are present and it is

impossible to say whether the plant had terminal or lateral flowering stems. The species present in Fiordland that the type could possibly represent are: *G. saxosa*, *G. montana* (sensu Allan 1961), *G. matthewsii*, *G. lineata*, *G. divisa*, and *G. bellidifolia*. *G. saxosa* was also collected at Dusky Sound by the Forsters. *G. matthewsii* is closest to *G. montana* in size, but some differences exist even on incomplete specimens. The lectotype is too tall for *G. lineata* and too sparsely branched in the flowering stem for *G. divisa*. It is conceivable that the type represents *G. bellidifolia*. Collections of *G. montana* (sensu Allan 1961) have been made from the outer Fiordland Sounds area (e.g., Lake Fraser, Wet Jacket Arm, Dagg Sound, South-West Cape, Secretary Island). A drawing of the flower of the lectotype made by N. E. Brown conveys the shape of the calyx which is one of the best identifying features of *G. montana*, and from this drawing and from the size of the lectotype I conclude that the name *G. montana* has been correctly applied by subsequent botanists.

G. montana is abundant throughout Fiordland and as far east as the Longwood Range and probably the Eyre Mountains. In Western Otago, it is less common, and is known from the Humboldt Mountains, Wilkin Valley, Mt Earnslaw, Cascade Valley, Gorge River. In South Westland it is known from the Moeraki tops, Mt Fox, Franz Josef, Copland Valley, Cook River, Burster Range, and Alex Knob. In South Westland, it has a larger number of more slender flowering stems than Fiordland plants and is difficult to distinguish from *G. matthewsii* there.

Gentianella montana is a very variable species throughout its range and shows so much distinctive regional variation such that plants can often be identified as coming from an area as small as a single peak. However, it is also true that plants from widely separated localities can look very similar. For instance, the rhomboid leaf shape of plants from Southland resemble those of plants from the area from Westport to Punakaiki. Plants with a nearly orbicular lamina on long narrow petioles and stolons can be found from the Heaphy area to South Westland. Such plants are usually found in wet soils, while plants nearby on dry soils lack stolons and have leaves of a different shape. These differences appear to be environmentally influenced. In Central Westland, it is uncommon, and has been occasionally collected in Canterbury. It is abundant north of the Kelly Range.

The population of *G. montana* s. l. on the Kelly Range does not fit well within *G. montana* s. s. or var. *stolonifera*, the plants being larger vegetatively and in their floral dimensions. While the Kelly Range plants are as tall as those of *G. "Paparoa"*, they lack the yellow corolla tube and impressed leaf veins of *G. "Paparoa"*. The population lies 50 km to the south of the southern limit of *G. "Paparoa"*, separated by the the lower Grey and lower Taramakau valleys. I am unable to say whether the Kelly Range population has its origin

from populations of *G. "Paparoa"* to the north or from populations of *G. montana* to the south and for now, I include it within *G. montana* ssp. *montana*. Studies using biochemical or genetic markers might help in deciding its taxonomic recognition either as part of *G. "Paparoa"*, or as a subspecies of *G. montana*.

Gentiana tereticaulis was named by Petrie from plants collected at Lake Harris on the Routeburn Track. Plants growing at Lake Harris are tall biennial plants. *G. montana* in Fiordland is a mixture of monocarpic and polycarpic populations. Plants closely resembling the Lake Harris plants and the type of *G. tereticaulis* have a southern limit in south-west Fiordland (e.g., Secretary Island) and a northern limit at Mt Earnslaw. Plants at Homer Tunnel's West Portal (*D. Glenny* 6840, CHR 559402) are polycarpic while plants from Homer Tunnel's East Portal (*D. Glenny* 6842, CHR 559406) are monocarpic and resemble those from Lake Harris. *G. tereticaulis* has no distinctive features that would set it apart from *G. montana* and Petrie did not mention any, commenting only that it was intermediate between *G. tenuifolia* and *G. corymbifera*. I conclude that *G. tereticaulis* falls within the variation of *G. montana* seen in Fiordland and West Otago.

Gentiana townsonii and *G. montana* var. *stolonifera*

Cheeseman (1906) did not nominate single types for *Gentiana townsonii* and *Gentiana montana* var. *stolonifera*. For *G. townsonii* he listed collections by Bidwill and Lyall at Kew which he did not see, and by Townson from Mount Frederic, Mount Rochfort, and Mound Buckland. For *G. montana* var. *stolonifera*, he listed collections by Forster, Anderson, and Lyall from Dusky Sound, and by Townson from Mount Frederic, Mount Rochfort, and Mount Buckland. The Townson collections probably represent best what Cheeseman took to be these two taxa, and lectotypes should be selected from these. I am selecting types for both from Mt Rochfort at 3000 ft. The lectotype of *G. montana* var. *stolonifera* is labelled "in scrub", and represents, in my opinion, a shade form of the lectotype of *G. townsonii* from the same locality and same altitude. I do not believe that there are two taxa growing sympatrically at sites such as Mt Rochfort. Some, but not all of the plants in the type gatherings of both *G. townsonii* and *Gentiana montana* var. *stolonifera* are stoloniferous.

This stoloniferous form occurs on the granite mountains west of the alpine fault on the Tuhua Range, Hohonu Range, Mt Te Kinga (all granite batholiths), and is common throughout the Paparoa Range (mainly composed of granite), and the coastal ranges north of Westport as far north as the Glasgow Range (also mainly composed of granite or a sedimentary rock derived from granite). It is also found at low altitudes on pakihis. For instance, it occurs on the old beach surface of German Terrace near Westport at 120 m a.s.l,

where it has presumably spread from the granite ridge above at 650 m. Inland, it occurs on the Lyell Range (also granite) but at the Matiri Range (composed of limestone) and Lookout and Hope ranges (composed of granite), it becomes difficult to say whether *G. montana* represented there is the var. *stolonifera* or the southern alps form, as stoloniferous plants are rare.

G. montana var. *stolonifera* is extremely variable in its leaf size and shape, and plant structure. The commonest leaf shape is narrowly elliptical. This form is seen along most of the length of the Paparoa Range and at Stockton and Denniston plateaux. Specimens from the Glasgow Range have wider leaves as do plants from further inland on the "Turks Cap Range" and Hope Range. Specimens from Buckland Peaks on the northern end of the Paparoa Range are particularly large. Specimens from pakihi at German Terrace near Westport and the ridge above it, and at Tiropahi River, are very similar to each other and are taller than usual for *G. montana* var. *stolonifera*, with acute tips but wide leaves and a long petiole. Specimens from Sewell Peak at the southern end of the Paparoa Range share this leaf shape but are shorter and more branched plants.

Plants of *G. montana* that are stoloniferous have their southern limit at the Cascade Plateau in South Westland, and their northern limit in the Heaphy area and are generally found in high rainfall areas between these limits (Fig. 14). They are present in the Southern Alps in South and Central Westland, but are uncommon in mountains of Lewis Pass, Hope Range, Lookout Range, Marino Mountains, and Arthur Range and in the Cobb Valley. In this drier, eastern part of Nelson stoloniferous forms are invariably associated with peat soils on valley floors, lake margins, or on saddles.

In Nelson, the most common form of *G. montana* is a robust form that is more branched than Fiordland plants. This form is common on the Lockett and Peel ranges, Mt Arthur and Gordon's Pyramid, and Mt Luna.

A feature of some stoloniferous populations of *G. montana* and all plants of *G. vernicosa* examined is non-zig-zagged epidermal cell walls (Fig. 14). The non-zig-zagged epidermal cells occurs in specimens of *G. montana* from the Lookout Range, Hope Range, Matiri Range, Buckland Peaks, Mt Fleming, and Croesus Track. The three sites last mentioned are on the Paparoa Range to the south of the present range of *G. vernicosa*. An explanation for this could be hybridisation between *G. montana* and *G. vernicosa* in the past. The presence of populations without zig-zagged epidermal cells on the Paparoa Range would then indicate either that *G. vernicosa* was formerly more widespread, or that the product of such hybridisation extended its range south. Other evidence (e.g., molecular) is needed to decide this.

In view of the complex variation in *G. montana* in the South Island, including the widespread existence of stoloniferous forms in the South Island, it has to be asked whether the stoloniferous forms on the western granite ranges of North Westland and Nelson should be recognised at any rank. I re-examine this issue following presentation of a principal components analysis.

Gentianella vernicosa and *G. gracilifolia*

The type of *G. gracilifolia* is from the Lockett Range, Nelson and that of *G. vernicosa* from Mt Arthur, also Nelson. The type of *G. vernicosa* is a more robust plant than plants in the *G. gracilifolia* type gathering. The type of *G. vernicosa* has a mean leaf width of 4.8 mm ($n = 5$) and its width was stated by Cheeseman (1906) to be $1/6-1/3$ in, while in *G. gracilifolia* the mean leaf width is only 2.5 mm ($n = 4$) and Cheeseman (1906) gives the leaf width for this species as $1/10-1/8$ in which is c. 2.5–3.1 mm. Other collections indicate that much of the variation in leaf size is due to soil fertility. However, it appears that there is a wider leaved form in the area directly north and east of the Cobb Valley which the type of *G. vernicosa* represents. Other examples of this form are *R. Mason*, Ridge between Anatoki and Douglas ranges, CHR 34918, and *A. P. Druce*, Hoary Head, CHR 395907. The degree of variation in this species seems insufficient to justify recognition of two subspecies. The two names were published together and I have chosen the name *G. vernicosa*, as the leaf dimensions for *G. vernicosa* given by Cheeseman (1906) represent those found in the species better than those he gives for *G. gracilifolia*.

G. vernicosa is less variable than other species in the *G. montana* group and has the smallest geographic range. It occurs from Westhaven (Wanganui Inlet) in the north to the Anatoki area, Goulard Downs, Lead Hills, Snowdon, Lockett, Peel and Arthur ranges, with a southern limit at Mt Owen in the east and Mt Stormy in the west. The habitat of *G. vernicosa* is usually *Chionochloa australis* grassland, both on soils derived from granite and other rock types including marble. It also occurs in *Olearia colensoi* – *Nothofagus solandri* scrub (McLennan, CHR 429251), in crevices in marble, in alpine herbfield and rockland, and in wet infertile sites with *Sphagnum cristatum*. It appears to prefer soils of low fertility, both wet and well drained.

The Paparoa gentian

Gentianella "Paparoa" is very distinct in the field and is sympatric with *G. vernicosa*, *G. montana* and *G. montana* var. *stolonifera* over much of its range. There is no doubt that it is a distinct species. It is found on the Glasgow Range, Paparoa Range and has a southern limit

in Westland on Mt Brown in the Haupiri Range and in Canterbury on the Crawford Range, just south of the Hurunui River. Its northern limit is at Bald Hill near Karamea. The habitat of the Paparoa gentian is *Chionochloa pallens* tussockland on hillslopes and ridges, in soils that are generally more fertile than those in which *G. vernicosa* is found, but the two species meet where there are mosaics of *Chionochloa pallens* and *C. australis*.

The Paparoa gentian is distinct from *G. montana* by its considerably larger leaves which differ in shape from those of *G. montana*, and it is sometimes taller with thicker flowering stems. The caudex is much branched, but in this respect it is matched by *G. montana* in Nelson. The corolla tube of the Paparoa gentian is strongly tinted yellow, a feature not seen in any other New Zealand gentian species. The corolla is longer than that of *G. montana* (Table 20).

Table 20 Differences between the Paparoa gentian (*Gentianella impressinervia*) and South Island *G. montana*, sympatric species.

	<i>G. impressinervia</i>	South Island <i>G. montana</i>
Stolons	usually present	sometimes present
Caudex length (mm)	65–300	10–160
Lateral leaf veins	impressed	not impressed
Corolla length (mm)	(16–)19–24	13.5–20
Corolla tube colour	vivid yellow	white or green
Anther length (mm)	2.8–3.9	1.7–3.0

The Cobb gentian

The Cobb gentian was first collected in the Cobb Valley by F. G. Gibbs (*Gibbs 369*, CHR 118637, no date) who wrote on the label: "Gentian ? patula, plentiful in Cobb V. Has violet stripes when growing. Probably not patula". Cheeseman determined this specimen as *Gentiana patula* in a letter to Gibbs in 1905. A. P. Druce became aware of the taxon, and tag-named it *G. "Cobb"*, and also determined many specimens as this taxon from the St Arnaud and Travers ranges, and others from elsewhere as far south as Lake Tennyson.

In the Cobb Valley and at Lake Tennyson, this gentian flowers in early January, reflecting its low altitude (820 m and 1130 m). Its flowering precedes that of *G. tenuifolia* in the same habitat at the Cobb Valley by several weeks. In the alpine zone at c. 1400 m at Nelson Lakes, plants of the Cobb gentian flower later, in February and March.

The affinities of the Cobb gentian are not obvious. It has similarities to *G.*

tenuifolia, with which it is sympatric, particularly in its patent flowering stem leaves. It is also similar to *G. montana* which is also present in the Cobb Valley at Lake Sylvester and is common on the Salisbury Open immediately to the south of the Cobb Valley. With *G. montana* it shares the following features: the caudex may be long, with leaf scars, and the rosettes are multiple and on long caudex branches. This is a feature of all species of the *G. montana* group but none of the *G. spenceri* group. However, the Cobb gentian never has stolons, a feature most of the *G. montana* group have to some degree. *G. "Cobb"* is variably monocarpic and polycarpic, even at a single site. This is a feature shared by *G. montana* s. s. while none of the species of the *G. spenceri* group are ever polycarpic. The calyx lobes are usually convex-margined, whereas in the *G. spenceri* group they are often pandurate, although in *G. tenuifolia* they are concave-margined (Fig. 5). The pollen grains are semi-reticulate and do not help establish its affinities. Neither the flower length (corolla 12.0–15.4 mm long) nor the pedicel length (9–35 mm) places it in one or other group, these dimensions being intermediate. My conclusion is that the Cobb gentian belongs in the *G. montana* group and needs to be compared to *G. montana* s. l. *G. "Cobb"* has some features shared by both the *G. montana* group and the *G. spenceri* group: crimson tinting of the stem and abaxial leaf surface, purple corolla veins, and a stigma sometimes tinted purple.

The Lake Gault gentian

Gentianella "Gault" was recognised by Wardle (1975) who collected it at South Westland pakihi on peat soils dominated by *Empodisma minus*. Wardle at first identified his own collections of this as *G. patula* but later determined them as *G. aff. spenceri*. It shares with the species of the *G. spenceri* group a purple stigma, purple corolla veins and its biennial life cycle, but in all other respects resembles *G. montana*.

As with the Cobb gentian, *G. "Gault"* shows an affinity to *G. montana* in three respects: 1) in some specimens (e.g., *P. Wardle*, Omoeroa/Waikukupa plateau, CHR 203677A) the caudex branches, 2) The calyx lobes of *G. "Gault"* are convexly tapering, whereas in *G. spenceri* the lobes are pandurate (Fig. 5), 3) *G. "Gault"* shares with *G. montana* var. *stolonifera* an open pakihi habitat, rather than the forest and scrub habitat of most members of the *G. spenceri* group. There are only two collections of this candidate taxon available, both from the same locality, at Lake Gault. Similar specimens from the Cascade Plateau were not flowering when collected.

Principal components analysis

A PCA including all members of the *G. montana* group was done with four objectives: (1)

To determine whether *G. montana* var. *stolonifera* can be discriminated from *G. montana*; (2) to determine whether *G. "Gault"* is distinct from *G. montana*; (3) to determine how distinct North Island populations of *G. montana* are from South Island populations; and (4) to find how distinct *G. "Cobb"* is from *G. montana*.

Fifteen characters were used and 56 specimens scored. They included five specimens of *Gentianella vernicosa*, seven of *G. impressinervia*, seven specimens of the Cobb gentian, five specimens of *G. montana* from the North Island, six of *G. montana* var. *stolonifera* from the Paparoa Range and ranges north of Westport, and two of *G. "Gault"*. The remaining 23 specimens were of *G. montana* from throughout the South Island, including a specimen representing the Kelly Range population, stoloniferous forms of *G. montana* from Nelson, Central and South Westland, and specimens from the Hope and Lookout Range representing populations of intermediate appearance between *G. montana* var. *stolonifera* and *G. montana* s. s.

Principal component I accounted for 42% of the total variance and high values on this axis were caused by large flower parts and large plants (Fig. 15). These characters were split by component II (explaining 14% of the variance) into a group of floral characters (e.g., anther length, corolla length, and calyx length) that had high component II scores and vegetative characters (e.g., leaf length, plant height, leaf width) that had low component II scores. The only character that was independent of these two groups was flower number (Fig. 16). Principal component III accounted for 11% of the variance, and is not presented as it did not assist in discriminating the groups.

All but one specimen of *Gentianella vernicosa* formed a group distinct from all others, reflecting the distinctness of this species. The specimen that did not fall close to the others was an unusually large specimen from Mt Owen (*D. Glenny* 7367, CHR 449993). Specimens of *G. "Paparoa"* formed a group in the analysis with the exception of an unusually small specimen from Mt Technical (*M. Newfield*, CHR 526413) which in other respects is undoubtedly *G. "Paparoa"*. A large specimen of *G. montana* from Central Westland (*P. Knightbridge*, McArthur Range, CHR 526438), fell within the area of the scatterplot occupied by *G. "Paparoa"*.

Gentianella montana occupies the largest area on the scattergram as expected from its already noted variability. Nelson, Westland, and Southland specimens are mixed, confirming that *G. montana* should not be split by separation along a north-south axis, although the specimens with the largest dimensions are from Nelson (Arthur and Balloon Hut), in accordance with observations that *G. montana* is particularly large there. A specimen from Lake Harris, the type locality of *G. tereticaulis*, is at the centre of the area of

the scattergram occupied by *G. montana*.

Gentiana montana var. *stolonifera* lies within *G. montana* on the scattergram, with all samples occupying one end of the area occupied by *G. montana*. The problem of distinguishing stoloniferous populations of *G. montana* from the Southern Alps from those of Nelson and Central and South Westland, is reflected in the scattergram. Specimens of *G. montana* that have similar component scores to *G. montana* var. *stolonifera* occur over a wide geographic area from Lake Sweeney in South Westland, Lake Wapiti in Fiordland, Mt Mason in the Haupiri catchment of North Westland, and Island Pass between the Clarence and Wairau Valleys. On the edge of the area occupied by *G. montana* var. *stolonifera* lie three specimens, two from the Lookout Range in Nelson, and one from the Longwood Range in Southland.

The analysis confirms that there is a basis for considering *G. montana* var. *stolonifera* to be distinct. In my opinion, it is a distinct element in *G. montana*, and deserves taxonomic recognition. Its sole defining character, present in all populations, is the presence of stolons. However, stoloniferous plants are found in a few other parts of the South Island (list). I have therefore decided to continue to recognise it as a variety, even though in the field, it seems more distinct than this would indicate. Molecular studies are needed to establish the distinctness of this variety.

The two specimens of the *G. "Gault"* fall within the area of the scattergram occupied by *G. montana* s. s. and have very similar component I and II scores to plants from the type locality of *G. tereticaulis* at Lake Harris. The analysis gives no support for the recognition of *G. "Gault"*. Its distinguishing characters are its coloured corolla and purple stigmas and the monocarpy of the plants, an uncommon state for *G. montana* in South Westland. A comparison of 13 quantitative characters of *G. "Gault"* and *G. montana* (not presented) shows it falls within the range of *G. montana* with the exception of plant height and corolla lobe length. The *G. "Gault"* population is therefore treated as belonging in *G. montana*.

North Island plants of *G. montana* appear between *G. vernicosa* and *G. montana* var. *stolonifera* in the scattergram but are closer to var. *stolonifera*. One of the five samples fell within the area of the scattergram shared by *G. montana* s. s. and var. *stolonifera*. The North Island populations are not completely separated from South Island populations of *G. montana* s. l., but the separation is better than that between subsp. *montana* and var. *stolonifera*. North Island populations of *Gentianella montana* differ from *G. montana* s. s. in three qualitative characters: the plants are uniformly monocarpic, they always have coloured corolla veins and have a blue or violet stigma. Of 16 quantitative characters compared, eight differ significantly (Table 21). On the grounds of the partial separation of North Island

populations from the rest of *G. montana* in the PCA, the differences in means, and the consistent qualitative differences, the North Island populations are recognised as a separate subspecies of *G. montana*, ssp. *ionostigma*.

Table 21 Comparison of South Island and North Island *Gentianella montana*.

	South Island <i>G. montana</i> (<i>n</i> = 21)	North Island <i>G. montana</i> (<i>n</i> = 5)	<i>t</i> (<i>n</i> = 5)
Plant height (mm)	130–260–490(–570)	75–140–220	2.8 **
Flowering stem diameter	1.4–3.2–4.8(–5.2)	1.5–2.3–2.5	3.6 ***
Leaf length (mm)	23–47–81	19–26–35	4.1 ***
Leaf width (mm)	6–11–18	5.3–7.2–9.5	4.2 ***
Petiole width (mm)	1.5–3.5–7.1	1.3–2.1–3.0	3.7 ***
Flower number	4–27–48(–120)	75–140–220	1.1 -
Calyx lobe length	4.4–6.8–8.7	4.7–6.3–8.2	1.9 -
Calyx lobe width	2.0–2.8–3.4(–4.0)	2.0–2.4–2.9	2.7 **
Corolla length (mm)	13.7–17–24	12.3–15–18	1.1 -
Anther length	1.7–2.5–3.2	1.8–2.1–2.8	3.1 **
Filament width	0.6–1.1–1.8	0.75–0.85–1.0	2.4 **
Ovules per ovary	32–53–88	32–58–75	1.4 -

Gentianella patula

The Cobb gentian occupies a distinct area on the scattergram, with similar component I scores to *G. vernicosa*, as both are small in their vegetative and floral parts. Specimens of *G. "Cobb"* had very large numbers of flowers (a mean of 76 per plant, compared to a mean of 26 per plant for *G. montana s. s.*), and this helps separate it from *G. montana*. The six specimens from the Cobb Valley, Nelson Lakes and Lake Tennyson clustered, but a seventh from Hare Creek in the upper Wairau Valley (A. P Druce, CHR 410232), determined by A. P. Druce as *G. "Cobb"*, had different component scores from the others.

Cobb Valley plants and Nelson Lakes alpine plants differ in several respects. The Cobb valley floor and the Lake Tennyson populations have coloured corolla veins, but the Lake Sylvester, Moa Park, and Nelson Lakes populations do not. The Cobb Valley and Lake Tennyson populations begin flowering at the start of January, and at both sites they may flower again in March. At Lake Sylvester (1325 m) the plants flower in mid-January to mid-

February. At Nelson Lakes, at altitudes between 1300 and 1600 m, flowering peaks in February and March. This spread of flowering times is what might be expected for a species with a wide altitude range.

There is a disjunction of 75 km between the northern populations at the Cobb Valley, Lockett Range, Canaan, and Moa Park and the southern populations at Nelson Lakes to Lake Tennyson (Fig. 17). The mountains that lie in this 75 km gap are the Arthur Range, Marino Mountains, Hope, and Lookout ranges. The wide upper Buller River Valley and the old glacial valley of the Rotoiti and Wairau Glaciers at Tophouse also lie within this gap. *G. montana* is present in the gap and it seems possible it has displaced the Cobb gentian there. Conversely, *G. montana* is not present on the St Arnaud and Travers ranges.

To determine whether these disjunct populations belong to the same taxon, specimens from the Cobb Valley, Lake Sylvester, and from Nelson Lakes to Lewis Pass were compared for four characters, plant height, number of flowering stems per plant, calyx lobe length and calyx lobe width, measured from herbarium specimens that were not rehydrated (Table 22). None of the means differ significantly (t-values not presented). These populations are therefore treated as a single entity.

Table 22 Comparison of the Cobb gentian at the Cobb Valley, Lake Sylvester and Nelson Lakes populations using four characters.

	Cobb Valley (<i>n</i> = 15)	Lake Sylvester (<i>n</i> = 4)	Nelson Lakes to Lewis Pass (<i>n</i> = 26)
Plant height (mm)	(60–)150–210–290(–340)	160–180–210	(70–)110–200–230(–280)
Number of flowering stems	2–6–13	3–14–19	1–8–35
Calyx lobe length (mm)	3.6–4.7–5.1	4.0–4.4–5.1	3.0–4.4–6.0(–6.6)
Calyx lobe width (mm)	1.6–2.0–2.3	2.0–2.1–2.2	1.6–2.0–2.4(–2.9)

G. montana and the Cobb gentian were also compared using the samples and characters that were used in the PCA. Ten sample means differ significantly: stem diameter, leaf width, petiole width, calyx length, calyx lobe length, nectary distance, filament length, filament width, anther length, and ovule number (Table 23). However, in all of the ten characters there is overlap with *G. montana s. l.* Despite the visual distinctiveness of the Cobb gentian, the lack of consistent qualitative differences such as corolla colour makes it difficult to provide satisfactory key couplet to differentiate it from *G. montana*.

Table 23 Comparison of the Cobb gentian and *Gentianella montana* s. s.

	<i>G. patula</i> (<i>n</i> = 6 or <i>n</i> = 30*)	<i>G. montana</i> s. s. (<i>n</i> = 26)	<i>t</i>
Plant height (mm)	(60-)135-214-370*	130-254-570	1.9 -
Stem diameter (mm)	1.1-1.94-2.4(-3.6)	1.36-3.14-5.3	5.2 ***
Leaf length (mm)	18-32-44	45-46.8-81	2.7 **
Leaf width (mm)	3.5-6.5-9.0	5.5-10.2-18	4.7 ***
Petiole width (mm)	1.5-1.9-2.5	1.5-3.4-7.1	3.7 ***
Flowers per plant	(3-)40-76-126	4-26-120	3.9 ***
Pedice l length (mm)	9-16.5-27(-35)	11-22.1-33	1.3 -
Calyx length (mm)	5.1-6.7-8.5	7.1-9.45-12	6.0 ***
Calyx lobe length (mm)	3.4-4.3-4.5(-6.0)*	4.4-6.8-8.7	3.0 ***
Calyx lobe width (mm)	1.8-2.1-2.3(-2.6)*	2.0-2.75-4.0	5.4 ***
Corolla length (mm)	5.9-12.7-16	13.7-16.9-24	3.1 **
Nectary distance (mm)	0.3-0.6-0.7(-0.8)	0.3-0.8-1.5	2.5 *
Filament length (mm)	4.5-7.5-8.8	6.5-9.1-11.0	2.9 **
Filament width (mm)	0.7-0.9-1.0	0.6-1.1-1.8	1.8 -
Anther length (mm)	(1.7)1.9-2.1-2.4	1.7-2.55-3.2	3.5 ***
Ovule number	24-33-44	32-52-88	5.7 ***

The Cobb gentian is an important entity, abundant in the alpine zone of the Travers and St Arnaud ranges, and in the Cobb Valley, that should not be submerged in *G. montana*.

Further field work and molecular evidence would be valuable to help clarify its relationship to *G. montana*.

Gentiana bellidifolia var. *patula* was described by Kirk. There are two syntypes at WELT as indicated by Kirk’s use of red ink for the names on the labels. One of these, *J. B. Armstrong*, Canterbury Alps, is a specimen of *Gentianella serotina*. If chosen as the lectotype, *G. serotina* would be a synonym of *G. patula*. The second syntype, *T. Kirk*, from Rotoiti, WELT 47583, is in my opinion, the Cobb gentian. If this specimen is chosen as the lectotype, *Gentianella patula* is the name of the Cobb gentian. Kirk’s description has features of both species: numerous shortly decumbent stems and oblong-spathulate leaves are features of the Cobb gentian, while large flowers are a feature of *G. serotina* but not the Cobb gentian. Kirk’s description omits mention of the one feature that would decide the

issue, the presence or absence of a terminal flowering stem. In the absence of any deciding factor in the protologue, it is preferable to choose the Rotoiti syntype as lectotype for the following reasons. *G. serotina* is a well established name that is well understood. Mark & Adams (1973, plate 74) in their widely used work applied the name *G. patula* to the Cobb gentian. The use of the name *G. patula* for the Cobb gentian makes a new name for the Cobb gentian and for *G. serotina* unnecessary. The Rotoiti syntype is therefore chosen as the lectotype.

Adams (1995, p. 977) believed that the type of *G. patula* should be a specimen seen by Hooker (1864, p.191) for his *G. saxosa* var. β and that *Sinclair and Haast*, Sinclair Range and elsewhere, Southern Alps should be the type. I disagree. Firstly, Hooker's *Gentiana saxosa* var. β is not a validly published name as it lacks an epithet. Secondly, the type of *Gentiana bellidifolia* var. *patula* must be a specimen seen by Kirk. It is unlikely that Kirk saw Kew specimens. Of the five species and six varieties of *Gentiana* described by Kirk in 1895, nine were described from his own collections, and two were described from collections made by Spencer and Potts, all now held at WELT.

In summary, the classification of the *G. montana* group presented here differs substantially from that of Allan (1961) (Table 15). *G. gracilifolia* is a new synonym of *G. vernicosa*, and *G. tereticaulis* is a new synonym of *G. montana*. North Island populations of *G. montana* are recognised as a new subspecies, subsp. *ionostigma*. I continue to recognise *G. montana* var. *stolonifera* as a variety within *G. montana* ssp. *montana*. *G. townsonii* is a synonym of this variety. In addition, there is a new distinct species in Buller area, *G. impressinervia*, that is sympatric with *G. montana* and *G. vernicosa*. *G. patula*'s identity is established through lectotypification. Two small populations of distinctive plants, from the Kelly Range, and on South Westland pakihi near the Waikukupa River are placed into *G. montana* subsp. *montana*.

The *G. spenceri* group

This group is comprised of three named species, *G. spenceri*, *G. tenuifolia*, and *G. chathamica*. There are three other candidate taxa. A. P. Druce, in determinations on CHR specimens, recognised *Gentiana* "stellar" of the Nelson ultramafic zone, and *Gentiana* "volcanic plateau" of the North Island. Specimens that I considered intermediate between *G. spenceri* and *G. tenuifolia* from Central and South Westland were investigated. Characteristics of named and candidate taxa are compared in Table 24.

Table 24 Comparison of members of the *Gentianella spenceri* group.

	<i>G. spenceri</i>	<i>G. tenuifolia</i>	<i>G. stellata</i> (<i>G</i> °, "stellar")	<i>G. chathamica</i> ssp. <i>nemorosa</i> (<i>G</i> °, "volcanic plateau")	<i>G. chathamica</i> ssp. <i>chathamica</i>
Plant height (mm)	(85-)100-170-270	230-330-530	180-290-730	25-100-210(-300)	90-125-235
Stem leaf pairs	1-3	4-6	1-6	1-2	1-3
Leaf length (mm)	25-44-80(-93)	40-72-117	12-55-100	18-26.3-44	21-27.2-31
Leaf width (mm)	13-17.5-22	8.5-15-24	(3.7-)6.0-8.7-19	5-9.3-15	7-9.4-12
Leaves and calyx lobes recurved	no	no	yes	no	no
Flowering stem leaves	orbicular	ovate	ovate	ovate	ovate
Pediceal length (mm)	1.5-10	4-30	3-45	3.5-17	5-20
Calyx lobe length (mm)	5.3-9.3	4.0-5.9	3.8-8.2	4.2-6.1	4.7-5.7
Calyx lobe margins	smooth or serrulate	smooth/ serrulate	smooth/ serrulate	serrulate	smooth
Corolla length (mm)	9.3-11-14	9.8-12-17.2	10-17-23	4.5-7.1-9.8	5.1-8.3-11.5
Corolla colour	purple veins	purple veins	colourless veins	crimson veins	crimson veins
Anther colour	dark red	blue-black	yellow or blue-black	blue-black	purple-red
Anther length (mm)	1.1-1.14-1.3	1.3-1.8-2.1	1.7-2.2-3.1	0.4-0.74-1.1	0.5-1.1-1.4
Stigma colour	crimson	crimson/blue	colourless	crimson, blue or purple	colourless
Ovule number	(4-)22-28-33	18-33-53	18-43-68	9-18-29	22-37-60
Habitat	montane to subalpine forest	montane forest and forest margins	manuka shrubland	montane forest and forest margins	bracken fernland
Altitude (m)	610-1525	500-1260	180-900	750-1350	5-140

Gentianella spenceri has a distribution from the Heaphy area in the north to the granite batholiths of Mt Tuhua and the Hohonu Range in the south. It occurs west of the Main Divide as far south as the Whitcombe Valley. It is geographically and morphologically separate from *G. tenuifolia* which has a more eastern distribution, from the Pikikuruna Range and Cobb Valley in the north to the Craigieburn Range in the south. *G. tenuifolia* is found as far east as Parnassus and the Seaward Kaikoura Mountains. The two species differ most obviously in two respects: *G. spenceri* is small in stature (110-140 mm high), and has orbicular leaves that are petiolate (Fig. 18), while *G. tenuifolia* is tall (230-750 mm high) and has longer narrowly elliptical leaves without such a distinct petiole. Other differences are summarised in Table 25.

Table 25 Comparison of *Gentianella spenceri*, *G. tenuifolia* and the type of *G. tenuifolia*.

	<i>G. spenceri</i>	<i>G. tenuifolia</i>	type of <i>G. tenuifolia</i>
Plant height (mm)	(85–)100–270	230–530	310
Leaf length (mm)	25–80(–93)	40–117	125
Leaf width (mm)	13–22	8.5–24	32
Leaf apex shape	rounded	acute or rounded	rounded
Pedicel length (mm)	1.5–10	4–30	2.5–10 (in bud)
Calyx length (mm)	6.0–10.7	6.0–9.8	9.4
Calyx lobe length (mm)	5.3–12	4.0–5.9	6.8
Calyx lobe width (mm)	1.4–2.1	1.4–2.0	1.9
Anther length (mm)	1.1–1.3	1.3–2.1	1.7–1.8
Ovule number	4–33	18–53	46–60

A problem exists over the type of *G. tenuifolia* as the type locality at Lyell Creek in the lower Buller River valley is west of the known distributional limits of *G. tenuifolia* in Nelson and the nearest collecting sites to Lyell Creek are near Mt Owen, 42 km north east, and Rotoiti 60 km to the west. Although *G. tenuifolia* is mostly found in drier eastern parts of the northern South Island, it occurs in the Arahura Valley, an area of very high rainfall. The type of *G. tenuifolia* comes close to other specimens of *G. tenuifolia* used for comparison in its height, leaf dimensions, calyx dimensions and anther length (Table 25). It exceeds all other specimens of *G. tenuifolia* seen in leaf width (Fig. 18). Pollen from the type was studied, and 5.8% of the grains were malformed ($n = 300$), suggestive of a hybrid, but overall there is insufficient evidence to reject the name.

Principal components analysis

A principal components analysis was performed that included specimens representing all members of this group (Fig. 19 and 20). Four specimens of each taxon were included, with the exception of five for *G. spenceri*. Scores for each specimen were often averages of measurements from several plants. Seven specimens of the variable species *G. grisebachii* were included for comparison, as *G. "volcanic plateau"* has a strong resemblance to *G. grisebachii*.

The type of *G. tenuifolia* was added to the principal components analysis. Scores for

filament width and corolla length were not available because of the immaturity of the flowers, and average values for *G. tenuifolia* were substituted. The type falls close to several other tall *G. tenuifolia* specimens in the PCA scattergram.

Southern limits in Westland of G. spenceri and G. tenuifolia

Some specimens from South Westland and Central Westland which are difficult to determine may belong either in this group or in the *G. grisebachii* group. Seven of these specimens were included in the PCA. In the scattergram, specimens from Mt Fox, Franz Josef, the Windbag River, and Mt Tuhua have scores very close to *G. matthewsii* collected from the type locality at Lake Harris. Their high component II scores are partly due to their long pedicels, a characteristic of *G. grisebachii* s. l. All of these South Westland specimens lack a compact rosette, also a characteristic of *G. grisebachii* s. l. I conclude that no member of the *G. spenceri* group is present in South Westland.

In Central Westland however, there are specimens that have a robust flowering stem and resemble *G. tenuifolia*: *D. Glenny* 6930, Harman River, in *Podocarpus hallii* – *Griselinia littoralis* forest (CHR 530599) and *D. Glenny* 6935, in *Olearia ilicifolia* scrub (CHR 530604). These specimens are incomplete as their terminal flowering stems have been chewed off by browsing animals. Two specimens, *D. Glenny* 8492, Kelly Range, CHR 546093, and *D. Glenny* 6591, Mungo Hut, CHR 530616, are *G. spenceri* (Fig. 18) but as neither was collected in flower they are not included in the PCA. It is not clear where the southern limit of *G. spenceri* is in Westland, or whether *G. tenuifolia* is present in Central Westland and further collections are needed to establish this.

Gentianella "stellar"

Despite overlap with *G. tenuifolia* in the PCA (Fig. 19), *G. "stellar"* is a very distinct species on characters not used in the analysis. It is most similar to *G. tenuifolia*, and is probably derived from that species but is confined to soils derived from dunite, an ultramafic rock type. Both species are biennial, erect and tall, the terminal flowering stem is thicker than the lateral ones, flowers appear near the base of the plants in both species, and they have similar calyces (Fig. 5). *G. "stellar"* differs from *G. tenuifolia* in a number of respects: the anthers are yellow (not blue-black), the corolla and stigma are never coloured (the veins and stigma are purple in *G. tenuifolia*), the flowering stem leaves and calyx lobes are strongly recurved in *G. "stellar"* (they are not recurved in *G. tenuifolia*) and the corolla lobes are strongly reflexed after the flowers open (Table 26). The corolla is more deeply lobed than most other New Zealand *Gentianella* species (lobes extend c. 0.82 the length of the calyx). In

cultivation the leaves lose some of their thickness, but the calyx lobes and flowering stem leaves remain recurved. On the margin of the Wairau Valley access road to the Red Hills, *G. tenuifolia* is common on loess derived soils under manuka scrub and forest margins. *G. "stellar"* immediately replaces *G. tenuifolia* on ultramafic soils beyond the boundary of the rock types and is abundant on the Red Hills and further north to D’Urville Island, wherever ultramafic rock is exposed.

Table 26 Differences between *Gentianella stellata* and *G. tenuifolia*, parapatric species.

	<i>G. stellata</i>	<i>G. tenuifolia</i>
Corolla colour	veins colourless	veins purple
Leaf texture	thick, firm, and glossy	thin, soft, and dull
Rosette leaf and calyx lobe curvature	recurved	flat
Calyx lobe width (mm)	1.5–3.0	1.4–2.0
Calyx sinus hairs	sparse	absent
Nectary distance from corolla base (mm)	1.7–2.7	0–1.0

Gentianella chathamica

This species belongs in this group by virtue of its being biennial, its small size, its terminal flowering stem and the number of lateral flowering stems that arise from the leaf rosette, the crimson tinting in its leaves and stems, its coloured corolla veins and stigma, small flowers, small anthers, and short pedicels. It is distinct from both *G. spenceri* and *G. tenuifolia*.

North Island specimens determined as *Gentiana* "volcanic plateau" by A. P. Druce are similar to both *G. chathamica* and *G. spenceri* as all three are about the same height and the pedicels are short in all three, and like *G. spenceri*, *G. "volcanic plateau"* is found under light forest and in forest clearings. It is also very similar to *G. grisebachii* which in the North Island also occurs in this habitat.

In the PCA scattergram *G. "volcanic plateau"* differs from *G. spenceri* in components I and II. However, it overlaps with *G. chathamica*. Both *G. "volcanic plateau"* and *G. chathamica* are close to, but distinct from, *G. spenceri* in the analysis. Herbarium specimens confirm this view of the relationships of the three taxa. A comparison of *G. "volcanic plateau"* and *G. chathamica* using eight quantitative characters (Table 27) shows only three differences in floral dimensions between the two taxa: anther length (larger in *G. "volcanic plateau"*), ovule number (lower in *G. "volcanic plateau"*), and stigma colour.

While the mean number of flowering stems per plant differs very little between the two, plants of *G. "volcanic plateau"* with a single flowering stem per plant are much less frequent than in *G. chathamica*. The similarities and differences between *G. chathamica* and *G. "volcanic plateau"* are commensurate with their being subspecies of the same species.

Table 27 A comparison of *Gentianella chathamica* s. s. and *Gentiana "volcanic plateau"* (*Gentianella chathamica* ssp. *nemorosa*).

	<i>G. chathamica</i>	<i>G</i> ^a . "volcanic plateau"	<i>t</i> , <i>n</i> , significance
Plant height (mm)	100–125–210	25–97–210	2.8 (<i>n</i> = 16) -
Number of flowering stems	1–4.35–15	1–3.4–18	2.6 (<i>n</i> = 78) **
Plants with one flowering stem	70% (<i>n</i> = 78)	27% (<i>n</i> = 78)	not applicable
Leaf length (mm)	21–27.2–31	18–26.3–44	0.09 (<i>n</i> = 6) -
Leaf width (mm)	7.0–9.4–11.5(–22)	5.0–9.3–15.0	0.006 (<i>n</i> = 6) -
Calyx lobe width (mm)	1.5–1.8–2.2(–2.5)	1.2–1.7–2.1(–2.5)	9.5 (<i>n</i> = 16)***
Anther length (mm)	0.5–1.1–1.4	0.4–0.74–1.1	2.1 (<i>n</i> = 5)–
Ovule number	25–45–60	9–18–29	4.3 (<i>n</i> = 5) ***
Stigma colour	colourless	purple	not applicable

The inclusion of *G. grisebachii* in the PCA shows why in the North Island *G. "volcanic plateau"* and *G. grisebachii* are difficult to distinguish. Specimens of *G. grisebachii* have a very wide range of component scores, and a specimen of *G. grisebachii* from Lake Manapouri, Southland, has component scores very close to those of *G. "volcanic plateau"*. A specimen of *G. grisebachii* from Rimutaka Saddle, Wellington, has a much higher value for component II than *G. "volcanic plateau"* which translates to its having a higher ovule number, longer pedicels, and wider calyx lobes.

In summary (Table 15), the *G. spenceri* group has changed by the addition of one new species, *Gentianella stellata* (tag name *Gentiana "stellar"*) and one new subspecies, *Gentianella chathamica* subsp. *nemorosa* (tag name *Gentiana "volcanic plateau"*).

The *G. grisebachii* group

This group is made up of *Gentianella gibbsii*, *G. lineata* and the *G. grisebachii* species aggregate. Neither *G. gibbsii* nor *G. lineata* pose any taxonomic problems. Although *G. lineata* is polycarpic, it has other characteristics that strongly indicate membership of the *G.*

grisebachii group: narrowly triangular calyx lobes (Fig. 6) and pedicels that elongate after flowering finishes. *G. grisebachii* s. l., however, is one of the most variable species in the genus in New Zealand. For example, the smallest and largest specimens of the aggregate differ in leaf length by a factor of seven. Within *G. grisebachii* s. l. is a candidate taxon that A. P. Druce referred to as *G. "rimutaka"*.

Petrie (1912a, p. 184) in naming *G. matthewsii* from collections from Harris Saddle on the Routeburn track said, "This species is somewhat closely allied to *G. grisebachii* Hook.f., differing in the stouter, more erect stems and branches, the much larger flowers and the shorter broader calyx-lobes." Cheeseman recognised *Gentiana matthewsii* as a variety of *G. grisebachii*, stating that in comparison to *G. grisebachii* s. s., var. *matthewsii* has stouter and more erect stems, broader leaves that are more oblong, larger flowers, and calyx lobes that are shorter and broader. Allan (1961) added little to this (Table 28).

Table 28 Differences between *Gentiana matthewsii* and *G. grisebachii* in Allan (1961).

	<i>G. grisebachii</i>	<i>G. matthewsii</i>
Branch position	laxly branched	with firmer branches
Leaf length (mm)	15–20	10–30
Leaf width (mm)	8–10	c. 6
Calyx lobe shape	linear-subulate	ovate-oblong to narrow-ovate
Corolla lobe shape	narrow-ovate to oblong, acute	subacute

G. matthewsii has not gained acceptance in New Zealand, with most specimens of this form being placed in *G. grisebachii*. A. P. Druce, however, on herbarium folders and determination slips at CHR, grouped many North Island specimens of this species aggregate into a further entity, *Gentiana "rimutaka"*, with a distribution in the Tararua, Rimutaka, Ruahine, and Raukumara ranges and wrote on each folder: "*G. 'rimutaka'* – none of these are *G. matth[ewsii]*". From his determinations on specimens at CHR it is apparent that at one time he thought *G. matthewsii* was also present in the North Island, but later he put nearly all *G. matthewsii*-like specimens from the North Island into the *G. "rimutaka"* folders.

I therefore considered three entities in the *G. grisebachii* species aggregate, with the character differences between *G. grisebachii* and *G. matthewsii* in Allan (1961) as a starting point for analysing variation in the aggregate. I attempted to find some geographic and morphological basis for two or three entities, accepting for the purposes of the analysis identifications made principally by A. P. Druce on CHR specimens. The null hypothesis was

that there is only one highly variable species. On the whole, coastal and montane plants are of the *G. grisebachii* type, while alpine plants are often, but not invariably, of the *G. matthewsii* type. For instance, plants of the *G. matthewsii* type are found on the hills of Otago Peninsula.

A metroglyph plotting leaf lengths of herbarium specimens onto a map of New Zealand (Fig. 21) shows that specimens mapped by leaf length do not fit a simple geographical pattern. Similar maps for leaf width and leaf length to width ratio show the same complex pattern (not presented).

Calyx lobe shape expressed as the width to length ratio of calyx lobes showed some geographic pattern (Table 29). Fig. 22 shows that specimens identified by A. P. Druce as *G. "rimutaka"* have broad calyx lobes, all specimens fitting into the upper end of the range with width to length ratios between 0.24 and 0.52. However, *G. grisebachii* and *G. matthewsii* specimens are mixed and more importantly, no geographical pattern is evident. A χ^2 goodness of fit test for calyx lobe length, calyx lobe width, and the ratio of these two performed on 58 samples showed that the combined data for all three putative taxa for these three characters fits a normal distribution ($p = 0.01$).

Table 29 Calyx lobe dimensions in the *G. grisebachii* aggregate. Dimensions are in millimetres and are sorted from narrowly triangular at the top of the table to ovate at the bottom of the table. The width to length ratio is given in the last column.

Identification	Locality	Calyx length	Calyx width	W:L
<i>G. grisebachii</i>	L. Ellesmere, Doyleston Drain	7.0	0.8	0.114
<i>G. grisebachii</i>	Awarua Bay	9.9	1.2	0.121
<i>G. grisebachii</i>	Rangitikei R, Ohutu stream	6.1	0.8	0.131
<i>G. grisebachii</i>	Cascade River mouth	6.0	0.8	0.133
<i>G. grisebachii</i>	Clarence Valley	5.1	0.7	0.137
<i>G. grisebachii</i>	Hooker Valley, terminal morain	7.0	1.0	0.143
<i>G. grisebachii</i>	Fagan Downs	8.0	1.2	0.150
<i>G. matthewsii</i>	Swampy Hill	6.9	1.1	0.159
<i>G. matthewsii</i>	Ringaringa River, Stewart Is	7.4	1.2	0.162
<i>G. matthewsii</i>	Waitutu	5.5	0.9	0.164
<i>G. matthewsii</i>	Maungatua	6.5	1.1	0.169
<i>G. matthewsii</i>	Supper Cove, Dusky Sound	7.1	1.2	0.169
<i>G. grisebachii</i>	Rangatikei River, the Narrows	5.8	1.0	0.172

Identification	Locality	Calyx length	Calyx width	W:L
G. matthewsii	Oreti Beach	5.7	1.0	0.175
G. grisebachii	Pouakai Range	5.1	0.9	0.176
G. matthewsii	Rees Valley	5.1	0.9	0.176
G. matthewsii	Mt Rakeahua Hut	9.0	1.6	0.178
G. matthewsii	Otaitai	5.0	0.9	0.180
G. matthewsii	Lake Monk	8.1	1.5	0.185
G. matthewsii	Rakeahua River	7.5	1.4	0.187
G. matthewsii	Wilmot Flat Hut	6.4	1.2	0.188
G. matthewsii	Weydon Burn	6.9	1.3	0.188
G. grisebachii	Okuku saddle	6.8	1.3	0.191
G. grisebachii	Matiri Range	6.2	1.2	0.194
G. grisebachii	Mt Tihia, SW of L.Taupo	5.6	1.1	0.196
G. matthewsii	Clinton-Mataura Rd	5.5	1.1	0.200
G. grisebachii	Oroua River	3.8	0.8	0.211
G. matthewsii	Hunter Valley	5.2	1.1	0.212
G. matthewsii	Flagstaff	4.2	0.9	0.214
G. grisebachii	Mt Oxford, Whites Creek	4.1	0.9	0.220
G. grisebachii	Two Thumbs Range	5.6	1.3	0.232
G. matthewsii	Lammerlaw Range, Teviot Swamp	5.6	1.3	0.232
G. grisebachii	Lewis Pass	6.0	1.4	0.233
G. matthewsii	Oreti R. near S.Mavora River	4.3	1.0	0.233
G. matthewsii	Marks Flat	6.4	1.5	0.234
G. grisebachii	L Georgina, Coleridge	4.6	1.1	0.239
G. matthewsii	Dome Burn	8.3	2.0	0.241
G. matthewsii	Colac Bay	7.0	1.7	0.243
G. matthewsii	Riverton-Invercargill	4.5	1.1	0.244
G. rimutaka	Tararua Ra, Mt Kariparoro	8.0	2.0	0.250
G. matthewsii	Taiaroa Bush	4.0	1.0	0.250
G. rimutaka	Mt Raukumara	5.0	1.3	0.260
G. matthewsii	Nevis Valley	5.3	1.4	0.264
G. grisebachii	Tarndale	5.5	1.5	0.273
G. matthewsii	Wilmot Pass	11.1	3.1	0.279
G. matthewsii	Lake Sweeney	6.0	1.7	0.283
G. rimutaka	Tararua Ra, Wainui Summit	9.7	2.8	0.289

Identification	Locality	Calyx length	Calyx width	W:L
<i>G. grisebachii</i>	Hunter Hills, Weaner Run	6.3	1.9	0.302
<i>G. matthewsii</i>	Wet Jacket Arm	8.5	2.7	0.318
<i>G. rimutaka</i>	Ruahine Ra, SW of Takapai	5.0	1.6	0.320
<i>G. rimutaka</i>	Tararua Ra, Te Matawai	5.3	1.8	0.340
<i>G. rimutaka</i>	Rimutaka Range	6.0	2.1	0.350
<i>G. rimutaka</i>	Tararua Ra, Mt Waiopahu	6.0	2.1	0.350
<i>G. rimutaka</i>	Raukumara Ra, Kopua-Tarati Ridge	4.2	1.5	0.357
<i>G. grisebachii</i>	Lake Sarah	8.6	3.1	0.360
<i>G. rimutaka</i>	Ruahine Ra, Whanua Huia Ra	4.1	1.6	0.390
<i>G. matthewsii</i>	Campbell Ck, Old Man Range	5.8	1.4	0.414
<i>G. matthewsii</i>	Tutuko Valley	5.8	3.0	0.517

A PCA was done using only the four characters already examined, leaf length, calyx lobe length, calyx lobe width, and the ratio of length to width. Principal component I accounted for 56% of the variance, and component II 32% of the variance ($n = 58$) and shows no clustering of the three entities (Fig. 23 and 24).

Flowering stem diameter was examined on freshly collected specimens, with identifications of my own, based partly on geography (Table 30). The number of localities sampled are few. A gap between *G. grisebachii* and *G. matthewsii* is filled by specimens from the Rock and Pillar Range and Rimutaka Saddle.

Table 30 Flowering stem diameter of fresh specimens in the *G. grisebachii* species aggregate.

Specimens examined (number of stems measured in parentheses)	Diameter (mm)
<i>G. matthewsii</i> , Blue Lake, <i>D. Glenny</i> 6385 (<i>n</i> = 2)	2.2–2.4
<i>G. matthewsii</i> , Lake Marian, <i>D. Glenny</i> 6838 (<i>n</i> = 2)	2.5–2.7
<i>G. matthewsii</i> , Gertrude Valley, <i>D. Glenny</i> 6843 (<i>n</i> = 4)	1.7–2.2
<i>G. matthewsii</i> , Harris Saddle, <i>D. Glenny</i> 6876 (<i>n</i> = 4)	1.6–2.2
<i>G. grisebachii</i> , Rock and Pillar Range, <i>N. Simpson</i> (<i>n</i> = 2)	1.4–1.5
<i>G. "rimutaka"</i> , Rimutaka Saddle, <i>D. Glenny</i> 6780 & 6805 (<i>n</i> = 7)	1.1–1.8
<i>G. grisebachii</i> , Siberia Valley, <i>B. Brown</i> (<i>n</i> = 1)	1.1
<i>G. grisebachii</i> , Manapouri, <i>P. Johnson</i> 1377 (<i>n</i> = 20)	0.6–1.1
<i>G. grisebachii</i> , Rees Valley, <i>D. Glenny</i> 6884 (<i>n</i> = 2)	0.7–0.8
<i>G. grisebachii</i> , Lake Sarah, <i>D. Glenny</i> 6905 (<i>n</i> = 1)	0.6

At two sites, plants of the *G. grisebachii* and *G. matthewsii* types are sympatric or nearly so, and these provide a test for the hypothesis that *G. grisebachii* and *G. matthewsii* are distinct species that maintain themselves as distinct despite their sympatry. Firstly, in the Garvie Mountains at Blue Lake, plants corresponding to the descriptions of *G. grisebachii* and *G. matthewsii* are found at each end of a lake c. 500 m long in very similar habitat. A comparison of the two is presented in Table 31. There is no overlap in any of the dimensions compared.

Table 31 Comparison of nearly-sympatric *G. grisebachii* and *G. matthewsii* plants at Blue Lake, Garvie Mountains.

	<i>G. grisebachii</i> (D. Glenny 6386)	<i>G. matthewsii</i> (D. Glenny 6385)
Branch lengths	10–13 cm	14–23 cm
Leaf dimensions	32 × 5.5–6.0 mm	39–65 × 9–15 mm
Calyx lobe dimensions	3.5–4.7 × 0.9–1.1 mm	7.5–7.7 × 2.3–2.5 mm
Calyx lobe ratio	0.19–0.27	0.29
Plant habit	branches lax, many (37 flowers)	branches erect, few, (3–)8–14 flowers
Habitat	<i>Hebe pauciramosa</i> , <i>Chionochloa rubra</i> , <i>Schoenus pauciflorus</i> , <i>Sphagnum cristatum</i> sedge shrubland on hummocky terminal moraine c. 30 m from lake margin.	<i>Hebe pauciramosa</i> , <i>Chionochloa rubra</i> , <i>Schoenus pauciflorus</i> , <i>Plantago</i> , <i>Sphagnum cristatum</i> sedge shrubland, 5 m from lake margin near outlet.

At a second such site in the Waimakariri Basin at Lake Sarah, plants grow amongst rushes on the lake shore and have broad calyx lobes and large leaves while only c. 30 m away, at a seasonally dry kettlehole tarn, small plants grow in the very short turf that have small leaves and have narrow calyx lobes. It appears that the more fertile swamp habitat not only affects the height of the plant and the leaf size, but that calyx lobe size is similarly affected (Table 32).

Table 32 Comparison of nearly sympatric *G. grisebachii* and *G. matthewsii* plants at Cass.

	<i>G. grisebachii</i> (D. Glenny 6905)	<i>G. matthewsii</i> (D. M. Post 357)
Branch lengths	3–8 cm	12–23 cm
Mean leaf dimensions (<i>n</i> = 4)	19 × 5.0 mm	33 × 8.6 mm
Calyx lobe dimensions	7.8 × 1.2–1.4 mm	8.6 × 3.1 mm
Calyx lobe ratio	0.15–0.18	0.36
Plant habit	branches decumbent, flowers 11–12	branches semi-erect, flowers c.8
Habitat	floor of ephemeral tarn, with <i>Juncus effusus</i> , <i>Agrostis tenuis</i> , <i>Gonocarpus micranthus</i> , <i>Polytrichum commune</i> .	among rushes on lake margin

Plants from these two sites were grown in the glasshouse side by side for 12 months to determine how much of the difference between them is genetic. The results are presented in

Table 33.

Table 33 Differences in leaf dimensions of wild and glasshouse plants of the *G. grisebachii* aggregate from Cass.

	<i>G. grisebachii</i> (Kettlehole Tarn)		<i>G. matthewsii</i> (Lake Sarah)	
Wild plants	12 × 3.8		53 × 9.0	
(length × width in	22 × 5.5	mean 19.0 × 5.0	33 × 9.0	mean 37 × 8.6
mm)	23 × 5.7		27 × 7.0	
			35 × 10	
Glasshouse plants	44 × 5.7		46 × 10.5	
(length × width in	49 × 8.6	mean 45 × 7.0	44 × 10.1	mean 51 × 11.5
mm)	40 × 5.9		63 × 14.0	
	47 × 7.6			

Leaf length increased in the Kettlehole plants by a factor of 2.4, but only increased in the Lake Sarah plants by a factor of 1.4. Leaf width increased in the Kettlehole plants by a factor of 1.4, and increased in the Lake Sarah plants by 1.3. Whereas in the wild the two forms do not overlap in leaf length, in the glasshouse they come very close, due mostly to extension of the petiole in plants from Kettlehole tarn. For leaf width, the glasshouse plants still do not overlap, and it remains possible to separate the two forms. There appears to be a significant genetic component to the difference between the two.

While most populations of plants of the *G. grisebachii* aggregate grow in swamps, flushes and bogs, it is notable that in the Rimutaka and Ruahine ranges, plants of this aggregate determined by A. P. Druce as *G. "rimutaka"* were commonly found under forest and scrub. Examination of herbarium material at CHR showed that 45% of specimens determined as *G. "rimutaka"* were collected from forest or scrub, whereas only 7.5% of specimens determined as *G. grisebachii* were found in this habitat (Table 34).

Table 34 Comparison of habitats of *G. "rimutaka"* and *G. grisebachii* in the North Island.

habitat	number of specimens of <i>G. "rimutaka"</i> at CHR	number of specimens of North Island <i>G. grisebachii</i> at CHR
alpine tarns	5	5
alpine herbfield	1	0
tussockland	4	15
scrub	5	1
forest (including forest openings)	4	1
pasture	1	0
riverbanks and cliffs	0	5

All plants of *G. "rimutaka"* that I saw on Rimutaka Saddle had crimson stigmas, and crimson corolla veins. In the South Island, of all plants that I saw fresh of the *G. grisebachii* aggregate ($n = 17$) only two specimens of *G. matthewsii* from Gertrude Valley (*D. Glenny*, 6843) and Forgotten River flats (*B. Brown*) had a purple stigma and neither had coloured corolla veins. As stigma and corolla vein colour are lost in dried specimens, it is impossible to say whether this feature of *G. "rimutaka"* is constant without further field work.

The calyx lobes of all specimens identified as *G. "rimutaka"* are wide relative to their length (ratio of width to length of 0.25 to 0.52) and are widest not at the base but mid-way up the lobe. This characteristic is shared with *G. matthewsii* and many specimens labelled as *G. grisebachii* from the South Island. Thus, in the North Island, a distinction can be made between *G. grisebachii* and *G. matthewsii*, but in the South Island, variation seems to be mainly habitat-based, and with a strong genetic component. On the whole, coastal and lowland plants are of the *G. grisebachii* type, while alpine plants are often, but not invariably, of the *G. matthewsii* type. An obvious exception to this altitudinal separation is plants of the *G. matthewsii* type plants on the Otago Peninsula hills.

To summarise, it is possible in the North Island to sustain the notion of a large form with wide calyx lobes (referable to *G. "rimutaka"* or *G. matthewsii*) being distinct from *G. grisebachii*. This North Island form does not differ from *G. matthewsii* in the South Island. In the South Island, however, *G. grisebachii* and *G. matthewsii* do not appear to be separable, for three reasons. Firstly, intermediates between the size extremes are more abundant than the extremes. Secondly, variation is habitat-based, not geographically-based but, and is partly phenotypic. This makes it impractical to classify wild plants as one or other taxon.

Because in the South Island no workable split between *G. grisebachii* and *G. matthewsii* can be made it seems unwise to recognise two forms in the North Island.

In summary, the classification of the *G. grisebachii* group has changed only by placing *G. matthewsii* into synonymy with *G. grisebachii* (Table 15).

The *G. bellidifolia* group

There are three named species in the group: *G. bellidifolia*, *G. amabilis*, and *G. serotina*. All of the species in the group has taxonomic problems. *G. bellidifolia* s. l. is a very widespread and very geographically variable species aggregate. *G. amabilis* is not very distinct from *G. bellidifolia*, but often grows with it. *G. serotina*, which has been assumed to be a distinct species since its description, is not distinct in any single character from *G. bellidifolia* s. l. In addition, two varieties within *G. bellidifolia* needed assessment: var. *pulchella* Kirk which needed lectotypification, and var. *australis* Petrie ex Cheeseman, which Druce (1974) considered to be a distinct species.

In addition to these three named species and two named varieties, there have been three other taxa proposed by Druce (unpublished). These are *G. "decumbent"*, *G. "long narrow leaves"*, and *G. "Red Hills Peat"* all of Nelson. In the case of *G. "decumbent"* and *G. "long narrow leaves"*, many herbarium specimens at CHR determined by Druce represent these two entities. However, no specimens at CHR were determined by Druce as *G. "Red Hills peat"* although the name appeared on his unpublished lists (e.g., Druce 1992b). This candidate taxon is probably represented best by A. P. Druce, Red Hills, habitat: "bog", CHR 273146, determined by Druce as *G. bellidifolia*. As the red tussock bog at the top of the Wairau Valley access road to the Red Hills is the only wetland in the otherwise dry and rocky Red Hills ultramafic area, it seems reasonably certain that this is the population believed by Druce to be distinct. I made collections of *G. bellidifolia* s. l. from this site. In my opinion, these plants do not differ from those collected from bogs elsewhere in Nelson, e.g., C. J. Webb 7666, Reverse Basin, Owen Range, habitat: "bog", CHR 283739, and M. J. A. Simpson 4168, saddle between Mole Stream and Bruce Creek, Nelson Lakes National Park, CHR 148807 and represent a form of very wet sites.

G. bellidifolia is the core of this group and most of the named and candidate taxa are the most obvious regional parts of this variation. The variation in *G. bellidifolia* s. l. is mainly seen in the leaf size and shape (Fig. 25), but also in the number of flowering stems per plant, and numbers of flowers per flowering stem. There is some variation in floral characters exists, but is much less obvious. In view of the lack of qualitative differences between the taxa, an attractive solution for the species aggregate would have been to regard

it as a single species with a number of subspecies, but in every case varying degrees of sympatry makes this solution impossible.

Gentiana bellidifolia var. *australis* was validly published by Cheeseman citing Petrie as the author. Cheeseman gave no explanation for nominating Petrie as author of the species, but six specimens in Petrie's herbarium (at WELT) have "var. *australis*" and "var. *australis* var. nov", and "at least a good var. var *australis*" in Petrie's hand on the labels, making it clear that Cheeseman was implementing Petrie's view of these specimens. Cheeseman cited no specimens, but gave the distribution as "high peaks on the mountains of the western coast of the South Island, from Karamea to Westport, Westland, and south-west Otago". There are three syntypes, from Mt Frederick and Buckland Peaks in Nelson, and from Kelly Range in Westland. There are also specimens from Petrie's herbarium annotated by Petrie as "var. *australis*" from Mt Peel and Gordons Knob in Nelson, Mons Sex Millia in Canterbury, and Bold Peak and the Rock and Pillar Range in Otago. Cheeseman's diagnosis of the variety is: "Stouter, often forming short dense patches 3–5 in. diam. Flowers abundantly produced, large, often quite 1 in. diameter." Allan (1961) notes that "Specimens collected by Petrie and others placed in herbaria under this name \pm agree with the above diagnosis". Druce (1974, p. 425) claimed that "it certainly is a distinct species" and he determined a number of specimens as *G. bellidifolia* var. *australis* or *Gentiana* "*australis*" from Nelson Lakes National Park. These specimens tend to have small, single rosettes and are often from rocky habitats.

Petrie's syntypes of var. *australis* are not particularly large plants. Most importantly, they are no larger than North Island plants. I am unable to agree with Cheeseman or Allan that populations of *G. bellidifolia* that occur on the western side of the South Island are larger than those elsewhere; in fact the opposite seems true. Westland specimens tend to be smaller than those from any other region (Fig 26). The largest-leaved populations are in Nelson, Marlborough, mid-Canterbury, and Central Otago. There is one difference between North and South Island plants of *G. bellidifolia* that could justify all South Island plants being called *G. bellidifolia* var. *australis*: the North Island plants uniformly have coloured corolla veins which the South Island plants do not have. This single difference seems insufficient to justify taxonomic recognition of the South Island plants and does not correspond to Cheeseman's diagnosis. I have chosen a specimen collected by Petrie on the Kelly Range as a lectotype for var. *australis*, on the grounds that it is the largest of the three syntypes, and so matches Cheeseman's diagnosis ("stouter") best.

G. bellidifolia var. *pulchella* Kirk has two syntypes at WELT, both determined with this name by Kirk. One is Kirk's own collection from Arthur's Pass at 3000 ft. (WELT

4717) and is *G. montana*, as it has terminal flowering stems, and one of the plants has stolons. The other is von Haast's collection from Meins Knob in the Rakaia Valley at 5000 ft. (WELT 4718). On this sheet there are three plants. The plant on the left is *G. montana* as it has a terminal flowering stem. The other two are *G. bellidifolia* as they have lateral flowering stems. Kirk's protologue gives the range as "South Island: Arthur's Pass, and other localities in the Canterbury Alps; 2,500 ft.–3,000 ft.". The von Haast collection does not match the protologue as it does not fall within the altitude range stated by Kirk. The Arthur's Pass collection matches the protologue in all respects and is nominated here as the lectotype. *G. bellidifolia* var. *pulchella* is, as a result, a synonym of *G. montana*.

G. amabilis was named by Petrie from a Southland specimen. Allan (1961) was doubtful as to its distinctness, indicated by his placing it in small type under *G. bellidifolia*. Mark & Adams (1973) stated that it "is now considered to be a uniform dwarfed form of *G. bellidifolia*, modified by its bog habitat." *G. amabilis* is sympatric with *G. bellidifolia* in Otago and Southland at many sites, but differs at these sites in its preference for wetter soils. This sympatry suggests that either *G. amabilis* is a form of *G. bellidifolia* growing in wetter sites or a species.

G. "long narrow leaves", as conceived by Druce, is an entity of the Nelson marble that outcrops from Hoary Head to Mount Owen in the Marino Mountains. This entity also seems to be present on the calcareous siltstones of Garibaldi Ridge. My observations in the Marino Mountains are that it is distinct from *G. bellidifolia* s. s. that is also present in this area but on moist peat soils of lower fertility that overlie schist within the marble terrain. This sympatry indicates that *G. "long narrow leaves"* is a distinct species. The obstacle to regarding it as a species are large-leaved populations of *G. bellidifolia* s. l. from greywacke and loess-derived soils in Nelson, Marlborough and Canterbury. It is doubtful whether the Canterbury and Marlborough large leaved populations share a common ancestor within *G. bellidifolia* as the the entity growing on marble in Nelson.

G. "decumbent" is very distinctive in the field. It is sympatric with *G. bellidifolia* s. s. in the sense that their distributions completely overlap, but I have not seen the two growing close together as the habitat of *G. "decumbent"* is usually well drained soils on ridges while *G. bellidifolia* s. s. is usually in flush and bog habitats. The problem in defining *G. "decumbent"* is that the distinctive field appearance of the plant is not reflected in the quantitative characters of leaf and floral dimensions.

Principal components analysis

A PCA was done for all candidate taxa of the group using 16 characters (Figs. 27 and 28). In

many cases, a mean was used where several measurements were taken from several plants making up a collection. Two ratio characters were used: the leaf length to width ratio, and the calyx lobe length to width ratio. The taxa sampled were: *G. bellidifolia* (17 specimens), *G. amabilis* (8 specimens), *G. serotina* (10 specimens), *G. "long narrow leaves"* from Nelson marble populations (10 specimens), long-leaved *G. bellidifolia* specimens from non-marble sites in Marlborough, Nelson, and Canterbury (7 specimens), *G. "decumbent"* (5 specimens), and *G. "Red Hills peat"* (2 specimens).

The component scores for the 16 characters were mostly concentrated in the same direction, with large plant, leaf and floral dimensions giving high values in component I (31% of the total variance) while large floral dimensions gave high scores and large plant and leaf dimensions gave low scores in component II (19% of the variance). Components III and IV accounted for 12% and 8% of the total variance respectively and are not presented. The analysis is interpreted under each species or candidate taxon.

Gentianella amabilis

In the field, *G. amabilis* appears to differ from *G. bellidifolia* in size, number of stems and number of flowers, and in the speckled purple colour of the leaves. *G. amabilis* often has solitary flowers on each stem, and has only a single flowering stem in 75% of specimens at CHR. In 35% of specimens, there was only one flower per plant.

In the PCA, *G. amabilis* specimens have low scores on principal component I due to their small size, and are intermediate to high on principal component II due to large floral dimensions and a very wide calyx lobe for its length, a conspicuous feature of the species (Fig. 6). No *G. bellidifolia* specimens from Otago were included in the analysis, so a regional comparison of *G. bellidifolia* and *G. amabilis* cannot be made.

A comparison of means for the 16 characters used in the PCA for *G. amabilis* and *G. bellidifolia* showed six that differed (Table 35).

Table 35 Differences in means between *Gentianella amabilis* and *G. bellidifolia*.

	<i>G. amabilis</i> (n = 8)	<i>G. bellidifolia</i> (n = 17)	<i>t</i> (n = 8)
Number of branches	1-1.7-3	1-4.0-11	2.8 **
Number of flowers	1-3.0-8	1-13.8-45	2.8 **
Calyx lobe width (mm)	3.1-4.0-4.7	1.7-3.0-4.2	3.4 ***
Calyx lobe ratio	1.6-1.9-2.4	1.4-2.2-3.4	2.9 ***
Corolla length (mm)	17-18.4-22.5	16-18.6-23	0.07 -
Nectary distance (mm)	0.6-1.2-1.8	0.4-0.85-1.1(-1.5)	2.2 *
Filament width (mm)	(0.9-)1.1-1.7-2.6	0.6-1.2-1.4(-1.9)	3.1 ***
Anther length (mm)	(1.7-)2.0-2.5-3.0	1.8-2.6-3.0	0.45 -

Druce's (1992a) contention that the flowers of *G. amabilis* are larger than those of *G. bellidifolia* is not supported by these data, as the mean corolla lengths do not differ. Two of the most obvious and taxonomically useful differences between *G. amabilis* and *G. bellidifolia* were of limited statistical significance: the number of branches per plant and the number of flowers per plant. The means for these two characters appear to be very different, but variation in these two characters is high (coefficients of variation of 80–100%). However, there are three significant differences in floral characters: calyx lobe width, the ratio of lobe length to width, and filament width. The two species overlap in their ranges for these three characters. Wide calyx lobes and filaments are a notable feature of *G. amabilis* flowers (Fig. 6).

Peter Johnson (pers. comm. January 1999) studied *G. amabilis* and *G. bellidifolia* at a site on the Old Man Range, near the Waikaia Bush Road, to help with the problem of whether these are distinct species. On 30 January 1999 at 1220 m he found *G. bellidifolia* on dry tussock slopes in full flower, while *G. amabilis* in a nearby bog was not yet in flower. He saw no intermediate plants. Near the crest of the range at 1420 m, Johnson found a bog within tussock grassland with *G. bellidifolia* in full flower on the bog margin and on low hummocks. *G. amabilis* was growing in the bog, with buds just appearing. Again, there were no intermediates visible. The two grow in a mosaic, as at Obelisk, with *G. bellidifolia* on the hummocks and *G. amabilis* in hollows between the hummocks. On 30 January 1998, Johnson made reciprocal transplants at this site, using peat squares of 100 × 100 mm and 150 mm depth. On 30 January 1999, he examined the reciprocal transplants and considered that there had been no change in either as the *G. amabilis* plants remained mottled and with

smaller leaves, while one of the two *G. bellidifolia* plants relocated had survived but had not changed and was flowering.

On the summit of the Old Man Range north of the Obelisk, at 1620 m on 21 February 1996, I collected *G. amabilis* and *G. bellidifolia* in hummocky terrain created by intense frost heave of the soil. The hummocks have dry grassland composed of *Poa colensoi*, *Zotovia thomsonii* and *Raoulia hectori*. *Gentianella bellidifolia* grows on these hummocks. Between the hummocks are linked pools and flushes with *Campyllum stellatum*, *Syntrichia robusta*, *Raoulia hectori*, *Psychrophila obtusa* and *Marchantia berteroana*. *G. amabilis* grows in these wet zones. The two gentians grew in very close proximity in this mounded topography and were both in flower, suggesting that there is overlap in flowering time.

Plants of *G. amabilis* from the Old Man Range were grown in the glasshouse. They kept their purple speckled leaves and purple-crimson petiole over a year, but after 6 years, while the petiole kept its colour, the speckling in the leaves was lost, suggesting that this pigmentation has partly a genetic basis and is partly a result of its wet habitat.

For *G. amabilis* and *G. bellidifolia* to remain distinct but grow in such proximity, there must be reproductive isolation by selfing, different flowering time, or an internal barrier to cross-fertilisation. Both species have large flowers, and attract pollinators such as syrphid flies, leaving the last two possibilities as the likely ones, assisted, according to Peter Johnson's observations, by a difference in flowering time.

G. amabilis has its northern limit at the Hawkdun Range and Dunstan Mountains. Specimens that resemble *G. amabilis* from north of this limit (e.g., on Mt Somers and Mt Nimrod) are *G. bellidifolia*.

Despite the lack of differences in the PCA and the comparisons of means, *G. amabilis* is distinct from *G. bellidifolia*.

Gentiana "decumbent"

This gentian is distinctive in the field for its large, symmetrically spreading plants, but there are few differences in leaves and flowers. Central to the question of whether it is a species or not is whether it is sympatric with *G. bellidifolia* s. s. The two are nearly sympatric at Lake Peel and the ridge above. *G. bellidifolia* occurs at Lake Peel at 1350 m in moist soils with *Bulbinella angustifolia* and bryophytes (Macmillan 89/46, CHR 327058) and on the ridge facing north-east above Lake Peel at 1430 m (J. A. Hay, CHR 75654). *G. "decumbent"* occurs in very well drained fellfield on the ridge to Mt Peel above these two sites at 1490 m (D. Glenny 7428), 1 km from the lake site. This degree of sympatry would be typical over

much of the range of *G. "decumbent"* with the two growing at some distance from each other because rarely do moist flush and bog habitats occur nearby well drained ridge fellfield habitats. *G. "decumbent"* is never abundant within its range, making it difficult to find a situation where it grows immediately next to *G. bellidifolia*. It is therefore difficult to know to what degree the two might be reproductively isolated.

In the PCA scattergram (Fig. 26), *G. "decumbent"* falls in the middle of *G. bellidifolia*'s range, giving no support for its recognition. A comparison of means between the two (Table 36) shows four significant differences, but in all cases there is overlap in the ranges.

Table 36 Comparison of means and ranges between *Gentiana "decumbent"* and *Gentianella bellidifolia*.

	<i>G^a. "decumbent"</i> (n = 5)	<i>G. bellidifolia</i> (n = 17)	<i>t</i>
Leaf length to width ratio	3.0-3.7-4.5	3.7-4.9-7.3	4.2 ***
Petiole width (mm)	2.3-2.8-3.6	0.8-1.7-4.6	3.7 ***
Calyx lobe l:w ratio	1.7-2.0-2.3	1.4-2.2-2.8	2.4 ***
Filament width (mm)	0.9-1.0-1.1	0.6-1.3-2.0	2.0 *
Nectary distance (mm)	1.0-1.9-2.3	0.4-0.9-1.4	4.0 ***
Anther length (mm)	2.3-2.6-2.7	1.8-2.5-3.0	0.25 -

In the field, mature plants of *G. "decumbent"* form a large multi-stemmed rosette about 300 mm diameter with flowers growing only on the perimeter of the rosette (Fig. 28, cf. *G. bellidifolia* Fig. 29). The flowering stem leaves are more numerous and more imbricate on the flowering stem than in other members of the *G. bellidifolia* group and are often appressed to the flowering stem at their base. The plants lack the purple-black pigment which is common in the *G. bellidifolia* group. They do not grade into any other form of *G. bellidifolia* anywhere within their range, and herbarium specimens are easily recognisable. For these reasons, and despite the paucity of differences between the two, I accept *G. decumbens* as a species.

Gentianella serotina

The type locality of *G. serotina* is Springfield, Mid-Canterbury. The northern limit of *G. serotina*, according to herbarium specimens, is at Lees Valley. Specimens from Banks Peninsula have a wider leaf than mid-Canterbury forms. Otago specimens of *G. serotina* are

larger than mid-Canterbury specimens (Fig. 25) and on some inland Otago ranges, they are difficult to separate from the large-leaved form of *G. bellidifolia* found there.

In the PCA, *G. serotina* specimens are only partly separated from *G. bellidifolia*, on the basis of having a higher leaf length to width ratio, a higher calyx lobe length to width ratio, and more numerous branches and flowers.

A comparison of means of *G. serotina* and *G. bellidifolia* was done using the PCA data set. Of the 16 characters compared, only one, the leaf length to width ratio, differed significantly at the 99.5% level (Table 37). Leaves of *G. serotina* are narrower for their length than those of *G. bellidifolia*, even though leaf length and leaf width differ less significantly. The relative narrowness of the leaves is one of the main ways in which the two can be distinguished in the field.

Table 37 Differences in means between *Gentianella serotina* and *G. bellidifolia*.

	<i>G. serotina</i> (n = 10)	<i>G. bellidifolia</i> (n = 17)	<i>t</i>
Plant height (mm)	78–187–300	30–112–140	2.6 *
Leaf length (mm)	43–66–112	16–39–80	2.4 **
Leaf length:width ratio	4.8–7.5–9.7	3.8–4.9–7.3	4.3 ***
Calyx lobe width (mm)	1.5–2.6–3.1	1.7–3.0–4.4	1.4 -
Calyx lobe l:w ratio	1.5–2.6–3.1	1.4–2.2–3.4	1.6 -
Corolla length (mm)	12.5–16.2–19.5	15.0–19.0–24.5	1.8 -
Nectary distance (mm)	0.3–1.3–2.2	0.4–0.85–1.5	2.3 *
Filament width (mm)	0.65–1.0–1.4	0.6–1.2–1.9	1.6 -
Anther length (mm)	1.8–2.3–3.2	1.9–2.6–4.2	2.0 -

G. serotina grows mostly in induced montane tussocklands and grasslands on outwash and river terraces and alluvial fans. *G. bellidifolia*, at least in Canterbury, is usually collected from peat soils. In Canterbury, *G. serotina* and *G. bellidifolia* do not meet as *G. serotina* is found at lower altitudes and has a more eastern distribution than *G. bellidifolia*. Where *G. bellidifolia* extends eastwards from the main divide in Canterbury, it occurs at altitudes of 1300–1700 m (e.g., Mt Cockayne on the Craigieburn Range, Mt Hutt, and Mt Somers). The nearest populations of *G. serotina* to these are in the intermontane basins of the Waimakariri, Rakaia and Ashburton rivers at 600–850 m.

In Otago and Southland, the same altitude separation generally occurs, but the two occur closer together and *G. serotina* is not confined to valley floors. For instance, in the

Eyre Mountains at Helen Peaks, at 1000 m *G. serotina* occurs in the valley (e.g., *B. Rance*, Cromel Stream, CHR 516252), while *G. bellidifolia* is found at 1450 m in alpine fellfield (e.g., *B. Rance*, Helen Peaks, CHR 516251). The same situation occurs in the Garvie and Hector Mountains. Herbarium specimens give the impression that the two are never found together. This separation in altitude may have arisen through *G. serotina* occupying natural grasslands and tussocklands on valley floors where frost kept these areas free of forest. If so, *G. serotina* has, since the removal of continuous forest from the mountain slopes, moved onto mountain tops of Mid Dome, Tennants Peak, Excelsior Peak and Tower Peak in Southland, all peaks of c.1200–1400 m. The situation of *G. serotina* and *G. bellidifolia* appears to parallel that of *G. corymbifera* subsp. *gracilis* and subsp. *corymbifera*, where subsp. *gracilis* has also occupied valley floor grasslands.

G. serotina was so named by Cockayne because of its late flowering, and Cockayne's type from near Springfield was flowering in the second week of April. Late flowering seems characteristic of mid-Canterbury populations where peak flowering is between c. 10 March and 10 April, the last plants to flower being those of lowest altitude on the Canterbury Plains. In Otago and Southland, flowering is earlier, peaking during February. This flowering time coincides with that of *G. bellidifolia*.

In the field, *G. serotina* and *G. bellidifolia* are not usually difficult to identify but some herbarium specimens from the Rock and Pillar Range, Old Man Range and the Hector Mountains are difficult to assign to *G. serotina* or *G. bellidifolia*. In other localities, a combination of plant height, leaf length and leaf width are enough to separate the two. *G. serotina* and *G. "long narrow leaves"* are also difficult to separate on floral and leaf characters but these two are widely allopatric. My conclusion is that *G. serotina* is distinct from *G. bellidifolia* over most of its range but I have reservations over the situation on the Old Man and southern Hector Mountains. As with *G. amabilis* and *G. "decumbent"*, differences in flower and leaf dimensions from *G. bellidifolia* are minor, and a key that will separate all specimens is even more difficult to construct. Useful differences for distinguishing the two species are summarised in Table 38.

Table 38 Useful differences that distinguish *Gentianella serotina* from *G. bellidifolia* (excluding the large-leaved forms of *G. bellidifolia*).

	<i>G. serotina</i>	<i>G. bellidifolia</i>
Leaf length (mm)	(32-)45-70-112(-160)	11-52-70(-80)
Calyx lobe width (mm)	<3.0	(1.7-)2.0-3.6(-4.2)
Leaf l:w ratio	rarely less than 6:1	usually less than 6:1
Plant height (mm)	commonly >140	usually ≤140

Gentiana "long narrow leaves"

The PCA scattergram (Fig. 26) shows plants of *G. "long narrow leaves"* as very different from any other samples, this difference being seen in high scores of principal component I due to their large size, their large leaves, and large floral dimensions. Plants similar to *G. "long narrow leaves"* from Rough Creek, Canterbury, and No Mans Creek, Marlborough, fall within the area of the scattergram occupied by *G. "long narrow leaves"* (Fig. 26), showing the difficulty of defining a Nelson marble species. The marble form and *G. bellidifolia* (including large-leaved non-marble forms) were compared using means from 13 characters from the PCA data set (Table 39). Seven of these means differ significantly, the strongest difference being in the leaf petiole width.

Table 39 Differences in means between *Gentianella angustifolia* and *G. bellidifolia* (including large-leaved forms from non-marble substrates).

	<i>G. angustifolia</i> (n = 11)	<i>G. bellidifolia</i> (n = 25)	<i>t</i>
Plant height	13-21.1-36	3-11.2-17.5	4.4 ***
No. of flowering stems	4-6.8-10	1-4.1-13	2.4, **
Leaf length (mm)	23-79-161	16-52-80	4.1 ***
Leaf width (mm)	10.0-13.0-15.5	4.2-9.7-15(-25)	4.3 ***
Petiole width (mm)	3.6-5.3-7.0	1.0-2.5-6.0	8.8 ***
Number of flowers	10-28.1-48	1-12.3-45	3.5 ***
Calyx length (mm)	9.0-13.7-18	6.6-9.7-14	4.0 ***
Calyx lobe length (mm)	5.6-9.4-12.5	3.8-6.6-10.0	3.1 **
Calyx lobe width (mm)	2.6-3.6-5.6	1.7-3.0-4.2	2.9 **

	<i>G. angustifolia</i> (n = 11)	<i>G. bellidifolia</i> (n = 25)	<i>t</i>
Ratio of lobe length to width	0.33–0.44–0.61	0.30–0.45–0.70	0.2 -
Anther length (mm)	1.9–3.0–3.9	1.8–2.5–3.0	1.3, -
Ovule number	35–60.2–80	21–40.8–60	3.8 ***

Other than on the Nelson marble, large leaved forms of *G. bellidifolia* are known in Marlborough at Wairau Peak, Mt Bounds, Altimarlock, Turks Head Saddle, Hodder Valley, and No Mans Creek; in Nelson at Mt Luna and Rainbow Skifield; in Canterbury from the upper Waimakariri catchment. The most distinctive of these forms are the much-branched, spreading plants with long but narrow leaves that grow on summit fellfield on Altimarlock. They could not be mistaken for *G. "long narrow leaves"* or *G. "decumbent"*. A collection from Turks Head Saddle (*M. J. A. Simpson* 879 & *R. V. Mirams*, CHR 80810, "fine shingle on saddle") strongly resembles the Altimarlock population and suggests there may be a distinct entity on fellfields in Marlborough. Further work may show that this Altimarlock type deserves recognition at some level, but at present there are too few collection sites in Marlborough to give an idea of its range and relationship to the *G. bellidifolia* populations that grow in moist soils in the region.

Near Arthur's Pass (Rough Creek, Punchbowl Falls Creek, Mt Williams), *G. bellidifolia* with leaves of normal dimensions are found in the alpine tussocklands while large-leaved plants can be found at lower altitudes, often near streams. Intermediates can be seen at these sites. Similar plants can be seen in Marlborough at No Mans Creek, but there large and small leaved forms occur within metres of each other (*D. Glenny* 6899, 1600 m, CHR 530572A-J). The large leaved non-marble forms at No Mans Creek and Arthur's Pass have narrower petioles (2.0–3.4–4.6 mm) than *G. "long narrow leaves"* (4.1–5.3–6.9 mm). The geographic and habitat variation in *G. bellidifolia* parallels that seen in the *G. grisebachii* – *matthewsii* complex. *G. "long narrow leaves"* appears to be a single entity on the Marino Mountains, Arthur, "Turks Cap", and Garibaldi ranges but probably is of different origin to the very similar large forms in Marlborough and Arthur's Pass. To describe *G. "long narrow leaves"* as a subspecies of *G. bellidifolia* would be appropriate if it were not for the fact that it grows alongside with *G. bellidifolia* s. s. without intermediates at Poverty Basin in the Marino Mountains. My decision is therefore to describe *G. "long narrow leaves"* as a species, *G. angustifolia*.

In summary, the classification of the *G. bellidifolia* group has changed by addition of two species, *G. decumbens* and *G. angustifolia*, and *G. amabilis* is confirmed as a species

(Table 15). *G. bellidifolia* is a very variable species as shown by the leaf diagram (Fig 26), but var. *australis* does not describe a distinctive part of that variation.

The *G. astonii* group

Gentiana astonii was described by Petrie from a specimen collected by B. C. Aston in the Waima Valley. By 1961 specimens that were assigned to this species had been collected from Ward Beach, the Clarence, Swale, and Dee rivers in Marlborough, from Mt Donald in North Canterbury, from near Taiko in South Canterbury, and from near Kurow in Otago (Allan 1961). Brian Molloy, from 1992 onwards, investigated these populations in the course of a study of plants endemic to eastern South Island limestone (e.g., Molloy et al. 1999). In 1998, Aaron Wilton collected a specimen of *G. astonii* from the Chalk Range with leaves that did not fit within the limits of Waima Valley *G. astonii* specimens. I compared all of these widely separated populations to determine their distinctness from each other. They are, in geographic order from north to south, *G. "Ward"* (Marlborough, hills immediately north and south of the Flaxbourne River mouth), *G. astonii s. s.* (Marlborough: Waima River, Benmore, Washdyke Creek, Mt Alexander), *G. "Chalk"* (Marlborough, Chalk Range, and North Canterbury, Whalesback), *G. "Brown"* (North Canterbury, Weka Pass, Mt Donald, Mt Brown, and Middle and South Dean), *G. "Manahune"* (South Canterbury, near Albury), *G. "Pareora"* (South Canterbury, near Cave), and *G. "Awamokoho"* (Otago, near Kurow).

The members of the *G. astonii* complex share certain features that establish them as a monophyletic group that is most closely related to the *G. bellidifolia* group. In common with *G. bellidifolia s. l.* they are all polycarpic, have lateral-only flowering stems, most have long, narrow leaves that are often V-shaped in section and recurved at the apex, most have minutely serrulate leaf and calyx lobe margins, narrowly triangular and acutely tipped calyx lobes. The corolla is large and white without coloured veins in most cases, although the Marlborough forms have violet tinting at the corolla lobe apices. The nectary is distant from the corolla base, and is well developed. The hypothesis, considered at the outset, that some of the populations are more closely related to other non-limestone species than to each other, is rejected. The candidate taxa are compared in Table 40.

Table 40 Comparison of seven candidate taxa of limestone on the eastern side of the South Island.

	<i>G. astonii</i>	<i>G. "Ward"</i>	<i>G. "Chalk"</i>	<i>G. "Brown"</i>	<i>G. "Manahune"</i>	<i>G. "Pareora"</i>	<i>G. "Awahokomo"</i>
Secondary branching	abundant	sparse to abundant	moderate	sparse	moderate	sparse to moderate	sparse
Caudex long and branched	sometimes	sometimes	-	-	-	+	-
Corolla sinus hairs	absent	present	absent/sparse	absent/sparse	present	absent	absent/rarely present
Rosette leaf blade shape	v. narrowly elliptical	narrowly elliptical	narrowly to very narrowly elliptical	linear	linear	narrowly elliptical to linear	linear
L:W ratio of leaves	7–13	4.0–4.7	4.2–7.4	11–12	10–16	6–14	17–27
Leaf length	24–32	13–17	12.5–13.5	58–78	30–60	42–75	69–83
Leaf width	1.8–2.8	2.8–3.7	1.7–3.1	4.8–6.9	2.8–4.1	4.4–8.8	2.6–4.1
Leaf apex recurved	no	no	no	yes	yes	yes	yes
Leaf margins	smooth	serrulate	serrulate	serrulate	serrulate	serrulate	serrulate
Leaves folded	flat	flat	flat/sl. keeled	keeled	sl. keeled	sl. keeled	keeled
Calyx margins	smooth	serrulate	smooth/sl. serrulate	serrulate	serrulate	serrulate	serrulate
Calyx lobes unequal	c. 0.82	c. 0.81	0.80–0.93	0.80–0.87	0.69–0.70	c. 0.5	0.86–0.88
Corolla length (mm)	10.4–14.7	14.5–15.2	11.5–13.0	9.4–11.6	11.7–13.8	14.6–19.0	13.5–17.1
Corolla colour	white	purple on lobe tips	purple on lobe tips	white	veins purple	white	white
Corolla lobe margins	slightly toothed	entire to strongly toothed,	toothed at apex	untoothed	slightly toothed	slightly toothed	slightly toothed
Corolla lobe margins finely serrulate	no	no	yes	yes	no	no	no
Nectary shape	wide V, deep pocket, with a toothed margin	wide V, deep pocket, with a toothed margin	V, a shallow divided pocket	crescent-shaped raised area, no flap	narrow V, raised area, no flap	narrow V to cup-shaped pocket, margin even	narrow V, margin even, occ. a deep pocket
Nectary distance (mm)	2.0–2.4	3.6–4.3	1.2–2.3	1.2–1.4	2.0–2.1	0.8–2.2	0.9–1.6
Anther colour	yellow or blue-black	blue-black	blue-black	blue-black	blue-black	blue-black	blue-black
Anther length (mm)	1.7–2.1	1.7–2.0	1.1–1.6	1.6–2.2	1.7–2.0	1.5–2.2	1.9–3.1

	<i>G.</i> <i>astonii</i>	<i>G.</i> "Ward"	<i>G.</i> "Chalk"	<i>G.</i> "Brown"	<i>G.</i> "Manahune"	<i>G.</i> "Pareora"	<i>G.</i> "Awahokomo"
Ovule number	27–29	19–28	13–22	11–21	17–21	14–24	(9–)14–34
Distribution	Marlborough	coastal Marlborough	North Cant., Marlborough	North Canterbury	South Canterbury	South Canterbury	Waitaki Valley

G. serotina appears to be the closest member of the *G. bellidifolia* group to the *G. astonii* complex. The features they share are purple-black flowering stems, serrulate calyx lobes, leaves that are narrowly elliptical, calyx lobes that are narrowly tapering (not seen in other members of the *G. bellidifolia* group). On these similarities, and because the Otago form of *G. astonii* at Awahokomo most closely resembles *G. serotina*, I hypothesise that *G. astonii* had its origin in a *G. serotina*-like ancestor in Otago.

Principal components analysis

A PCA of the seven candidate taxa was done. Between two and five specimens for each candidate taxon were used. The numbers of specimens sampled was severely limited by the number of herbarium specimens available for each, particularly for *G. "Awahokomo"* and *G. "Manahune"*. Eleven quantitative leaf and flower characters were used and the analysis performed (Figs. 31 and 32). Principal components I and II accounted for 38% and 21% percent of the variation respectively. Principal component III accounted for 16% of the variation, did not assist in separating the candidate taxa, and is not presented. Floral dimensions except for the distance of the nectary from the corolla base accounted for most of the variation in principal component I. Leaf length and width and nectary distance had the strongest effects on principal component II.

Two distinct groups can be seen: a group from the Kaikoura region and a group from Canterbury and Otago. *G. astonii* s. s. is a distinct group, while *G. "Ward"* and *G. "Chalk"* form a group but are mixed. All four Canterbury and Otago candidate taxa are mixed. *G. "Brown"* is spread over a wide part of the diagram on account of wide variation in leaf dimensions, although it has narrow variation in its floral dimensions. *G. "Awahokomo"* and *G. "Pareora"* have larger flowers than *G. "Brown"*. Both *G. "Manahune"* specimens fall close to the *G. "Brown"* specimen from Weka Pass.

Eight qualitative characters were then added and the analysis repeated (Fig. 32 and 33). The additional characters were for leaf margin and calyx margin serration, corolla colour, corolla sinus hair presence, corolla margin toothing, anther colour, and presence of a deep nectary pocket and toothing of the nectary pocket margin. The

qualitative characters were scored as 0, 1, or where a trait such as corolla colour was only slightly present, 0.5. Six components were significant, and consequently, the first two components account for only 25% and 18% of the variation respectively. Other components do not appear to assist in separating candidate taxa. Characters that produced components I and II were very scattered (not presented). Quantitative and qualitative characters from leaves and nectaries grouped together, but corolla coloration was independent of corolla length, and anther colour independent of anther length.

The two analyses agree in their main features. *G. astonii s. s.* maintained its separation from the other Kaikoura candidate taxa, but a Mt Alexander specimen is very close to a Ward Beach specimen because it has blue-black anthers. The Kaikoura region populations maintain their separation from the Canterbury and Otago populations as in the previous analysis. *G. "Brown"*, *G. "Manahune"*, and *G. "Pareora"* are mixed on the diagram, but *G. "Awahokomo"* is distinct from these three and from the Kaikoura region taxa.

Both PCAs show two main groups, a Kaikoura group and a Canterbury-Otago group. They indicate that *G. astonii s. s.* is separate from the Chalk Range and Ward Beach taxa, and do not support *G. "Chalk"* being distinct from *G. "Ward"*. The results do not support recognition of four Canterbury-Otago taxa, although the second analysis supports the recognition of *G. "Awahokomo"*.

G. astonii s. s. differs from *G. "Chalk"* and *G. "Ward"* in having longer narrower leaves without overlap in these dimensions (Table 41). The corolla is longer, but there is overlap in the ranges. The filaments are wider in *G. astonii s. s.* with no overlap. The leaf margin in *G. astonii s. s.* is never serrate, but is sometimes serrate in the other two. The corolla is less often tinted in *G. astonii s. s.* than the other two, and the anthers are yellow in *G. astonii s. s.* in the Waima catchment, but not in collections from Mt Alexander and Washdyke Creek. The most conspicuous difference between *G. astonii s. s.* and the other two candidate taxa is its longer narrower leaves, and justifies separating *G. astonii s. s.* from the other two at subspecies level.

Table 41 Comparison of *Gentianella astonii* ssp. *astonii*, *Gentiana* "Chalk" and *G.* "Ward".

	<i>G. astonii</i> s. s.	<i>G</i> ^a . "Chalk"	<i>G</i> ^a . "Ward"
Secondary branching	usually abundant	moderately abundant	moderately abundant
Leaf length (mm)	15.8–22.3–32	8.6–11.8–13.5	10–14.2–25
Leaf width (mm)	1.4–2.3–2.8	1.7–2.1–3.1	2.1–2.9–3.8
Leaf length to width ratio	7.0–9.3–13.3	4.2–5.6–7.4	3.6–4.9–6.3
Leaf margins serration	absent	weak to distinct	absent, weak, or distinct
Calyx length (mm)	7.0–10.0	5.8–10.2	4.4–7.1
Calyx margins serration	usually absent	usually weakly present	usually weakly present
Corolla length (mm)	10.4–17	6.2–15	8.1–15
Corolla lobe apices	usually white	usually tinted violet	usually tinted violet
Corolla margin teeth	usually absent	usually present	usually absent
Corolla sinus hairs	present	present (2) or absent (2)	present (3), absent (2)
Nectary distance (mm)	1.9–2.9	1.1–2.7	1.2–3.2
Nectary pocket	usually present	present but sts. weak	present
Nectary pocket margin	sometimes toothed	smooth	sometimes toothed
Filament width (mm)	0.7–0.8	0.4–0.6	0.3–0.6
Anther colour	yellow or blue-black	blue-black	blue-black

G. "Chalk" and *G.* "Ward" differ in only three respects. They differ slightly in leaf dimensions (Table 41). *G.* "Chalk" always has toothed corolla margins while *G.* "Ward" rarely has this feature, and *G.* "Chalk" has a smooth nectary pocket margin while *G.* "Ward" usually has teeth on the margin (present in three out of five samples). These differences seem insufficient to recognise two taxa at any level.

The PCA results indicate that the Canterbury-Otago populations are more distinct from the Kaikoura region populations than *G. astonii* s. s. is from the other Kaikoura region populations, and on this basis, it is appropriate to divide *G. astonii* s. l. into two species, *G. astonii* and a new species, *G. calcis*. The main differences between these two are that the Kaikoura species has smaller, flatter leaves, a bushier habit, calyx lobe margins less serrated, nectaries that are further from the corolla base and more deeply pocketed, and more tinting on the corolla lobes (Table 42). In many other characters the means in quantitative characters are nearly identical (e.g., flowers per

plant, corolla length ovules per ovary, and anther length). The Canterbury and Otago populations mostly have long, folded leaves, this folding being most pronounced in *G. "Brown"*. Of the four, only *G. "Manahune"* is bushy. The other three candidate taxa are rosette-forming gentians like *G. serotina*. The nectaries are closer to the corolla base and are less conspicuous than the Kaikoura populations, and in *G. "Manahune"* there is no pocket at all. The corolla is entirely white except in *G. "Manahune"* which has coloured corolla veins. The foregoing comparisons may suggest that *G. "Manahune"* is distinct from the other three southern taxa, but the PCA does not support this, as leaf and floral dimensions do not differ from those of some *G. "Brown"* plants. The PCA result using qualitative characters suggests that *G. "Awahokomo"* could be recognised as a species. The differences that separate *G. "Awahokomo"* from the other candidate taxa are its larger floral dimensions, and the lack of serration on the leaf and calyx margins. These differences are insufficient to justify more than subspecies rank.

Table 42 Comparison of *Gentianella astonii* (incl. ssp. *arduana*) and *G. calcis*.

	<i>G. astonii</i>	<i>G. calcis</i>
Bushy / rosette forming	bushy	rosette-forming in 3/4 subspecies
Leaf length (mm)	(8.6-)12.5-15.6-32	30-52.4-83
Leaf width (mm)	1.1-2.5-3.9	2.6-4.3-8.8
Leaf folding	plane	usually folded
Nectary distance (mm)	1.2-2.2-4.3	0.8-1.6-2.2
Leaf apex	not recurved	recurved
Corolla colour	white or tinted violet on outside of corolla lobes	white except in ssp. <i>manahune</i> which has purple veins

Some of the differences between the South Canterbury and Otago taxa reflect differences in habitat. *G. "Pareora"* grows in a moister habitat than *G. "Manahune"* and *G. "Awamokoho"*, as the limestone boulders it grows on are shady and damp and this is reflected in its long leaves, wide leaf lamina, and larger flowers, features that are kept in cultivation. *G. "Manahune"* grows in limestone cracks on the top of an escarpment in very sunny dry places, even having some preference for north facing aspects, and this bluff habitat may have induced the bushy habit that is also seen in the Marlborough taxa. *G. "Awahokomo"* grows mainly on the flat top of a large limestone outcrop in a very

exposed position (Molloy et al. 1999, fig. 2), and without the water seepage that must occur in vertical cracks on limestone bluffs. This situation is very similar that of *G. "Brown"* at Mt Brown in North Canterbury (Fig. 34) and the two share a simple rosette form and long folded leaves. These differences are retained in glasshouse plants.

An unexpected result is the disjunction of *G. astonii* ssp. *arduana* in view of the proximity of its Chalk Range population to *G. astonii* ssp. *astonii* in the Waima Valley. The rock substrate for both subspecies is Amuri Limestone (Druce & Williams 1989), and the bluffs provide the same habitat in both places, and on the coastal hills at the Flaxbourne River mouth.

These limestone taxa have a relative abundance of qualitative characters that probably results from a genetic bottleneck effect following dispersal to a new limestone outcrop, causing traits not otherwise seen in New Zealand *Gentianella* such as toothing on the nectary flap and corolla margin to become fixed. Some of these distinctive traits are inconsistent within taxa (e.g., yellow anthers in *G. astonii* s. s.). There is a paucity of material available for some candidate taxa, and the variation in these traits has probably been underestimated. While this study was in progress S. Moore found a North Canterbury population of *G. "Chalk"*, well south of Marlborough populations, that suggests further new populations of gentians on limestone outcrops in the South Island may be found.

To summarise, two species are recognised based on the similarities and differences shown by the two PCAs and comparison of characters. *G. astonii* is confined to the Kaikoura region and has two subspecies (ssp. *astonii* and ssp. *arduana*). *G. calcis* has a range from North Canterbury to North Otago and has four subspecies, ssp. *calcis*, ssp. *waipara*, ssp. *manahune*, and ssp. *taiko* (Table 15).

***Gentianella lilliputiana* group**

The position of *G. lilliputiana* with respect to other New Zealand species is uncertain. In common with members of the *G. divisa* group it has a terminal flowering stem and short wide calyx lobes. Its purple-spotted leaves and its purported hybridisation with *G. amabilis* indicates affinities with the *G. bellidifolia* group, but this is contradicted by its very small flowers, as the *G. bellidifolia* group have the largest flowers of the New Zealand species.

The pollen grain surface pattern of *G. lilliputiana* (Fig. 43) is very different from that of any other New Zealand gentian, and suggests that it has no close relationships with other New Zealand species. The pollen grain surface resembles that

illustrated for *G. magellanica* by Nilsson (1967, plate 24, 1–2). Nilsson made special comment under section *Andicola* of the reticulate surface of *G. magellanica* pollen grains and did not find this pattern in any other of the 16 South American species he sampled. The DNA sequence of *G. lilliputiana* reported below confirms its separation from other New Zealand species, but does not indicate its affinities.

Small examples of *G. magellanica* from the Falkland Islands (e.g., *D. M. Moore* 790, CHR 183097) resemble *G. lilliputiana* in being as small as 20 mm high, with 4-merous flowers, a calyx only 6.2 mm long (Fig. 6), a corolla 8.8 mm long, anthers only 0.7 mm long, the capsule small (8.5 mm long), but with many more ovules (24 per flower). DNA evidence shows that these similarities are not due to a close relationship (Fig. 35).

Phylogenetic analyses

Analysis of the morphological cladistic data matrix

Parsimony analysis of this data set (Appendix) showed no useful resolution, the strict tree being a comb with the exception of two major clades (Fig. 35). The first of these was the *G. bellidifolia* group (*G. amabilis*, *G. angustifolia*, *G. bellidifolia*, *G. decumbens*, and *G. serotina*), united by all members having lateral-only flowering stems. The second clade contained most species of the *G. divisa* group (*G. corymbifera*, *G. divisa*, *G. luteoalba*, and *G. magnifica*) but with the addition of *G. montana*, *G. impressinervia*, and *G. stellata* and was united by all members having thick flowering stems. In addition, the two annual species, *G. lilliputiana* and *G. filipes* formed a clade. There was no bootstrap support for any clade.

The analysis was repeated with the inclusion of one extra character, New Zealand geography, an ordered character that divided New Zealand into zones south to north. This extra character resulted in much more structure in the strict consensus tree (Fig. 36). However, the resulting tree does not come much closer to the relationships between the taxa as I see them. For instance, the three taxa that make up *G. montana* appear in three different clades.

The main reason for lack of resolution in the parsimony analysis is probably that there are almost no characters with state changes that do not show reversion in other parts of the tree. There are also too few characters for the number of species, but reanalysis with fewer species gave no better resolution. In the course of studying the group, and compiling the cladistic data set, and I drew an intuitive tree that represents my best estimate of the phylogeny of the group (Fig. 37). I used geographical

distribution of the species and their habitats as additional information in compiling this. Changes in life-cycle have been mapped onto this tree. The eight intuitively derived groups have been marked on the tree. The tree attempts to show how these eight groups might be related to each other, with the *G. saxosa* group at the base. *G. lilliputiana* is shown branching directly above the *G. saxosa* group. The *G. bellidifolia* group, the *G. astonii* group and the Australian species form a clade above this. The *G. divisa* group is shown as sister to the remaining four groups. The *G. montana* group is sister to the *G. spenceri* and *G. grisebachii* groups. Within each group, the branching structure attempts to show my estimate of relationships between the species. In some cases, I have not attempted this, either because of uncertainty over relationships or, in the case of the *G. bellidifolia* group, because speciation may have simultaneously occurred in different regions from the widespread species.

The tree (Fig 38) shows five or six changes in life-cycle. Either the ancestor of the New Zealand species was monocarpic, and on five occasions there was a change to polycarpy, or the ancestor of the New Zealand species was polycarpic and the change to monocarpy occurred six times in New Zealand. Some of these changes were at the base of major groups such as the *G. bellidifolia* and *G. astonii* groups, and at the base of the *G. spenceri* and *G. grisebachii* groups. In other cases, single species or subspecies have changed their life-cycle. For instance, North Island populations of *G. montana* are uniformly monocarpic while South Island populations are a mixture of monocarpic and polycarpic.

The DNA sequencing study

New Zealand, South American and Australian gentian species were sequenced to establish whether the Australian and New Zealand gentians belonged to the genus *Gentianella*, or some other genus. Four Northern Hemisphere sequences of *Gentianella* of Yuan & Küpfer (1995) were added to the data matrix. In ITS1 for the data set there were 41 variable sites (17% of the 240 sites), 16 of these variable within the Southern Hemisphere species. In ITS1 there was an indel of 2 bases in *G. saxosa* and an indel of 1 base in *G. diemensis*. The 5.8S region between the two spacers showed no variation. ITS2 for the data set had 50 variable sites (21% of 234 sites), 33 of these variable within the Southern Hemisphere species (Fig 39). In ITS2, *G. corymbifera* had a single base indel that was not shared with the other sample of *G. corymbifera*, and *G. serotina* had a single base indel. None of the indels were shared by species. ITS2 is more variable than ITS1 for Southern Hemisphere species and so was more useful.

The strict consensus tree of 10 000 shortest trees resulting from a parsimony analysis is a complete comb with no branches shared by all of the shortest trees, and is not presented. A graph resulting from a median network analysis is presented in Fig. 39 and is useful in showing the distances between species and the relationships between species that the data indicates. The graph shows a point around which most species are clustered, which can be interpreted as a point at which a very rapid radiation of species occurred. This rapid radiation explains why it is so difficult to discern the higher level relationships between the species groups.

The Australian species have four synapomorphies in ITS2 (highlighted, at positions 47, 48, 52, and 57). One of these, at position 52, is shared with *G. lineata* of New Zealand. The median network graph suggests a single dispersal to Australia early in the Southern Hemisphere radiation. There are no synapomorphies between the Australian species and any other species that would indicate whether the immediate origin of the Australian species was New Zealand or South America (possibly via Antarctica). The Australian species sampled represent a diverse sample according to relationships posited by Adams (1995). However, only by sequencing all the Australian species could the number of dispersals to Australia be established with certainty.

G. lilliputiana is the most distinct of the New Zealand species, due to a large number of autapomorphies. Unfortunately, it lacks any synapomorphies that would indicate its closest relatives.

The position of the South American species relative to the New Zealand species is not resolved as there are no synapomorphies that unite the South American species. The visual centre of the median network graph in Fig 40 at which *G. serotina*, *G. bellidifolia*, and *G. cerina* are positioned has both New Zealand and South American species radiating from it in two places (*G. myriantha* and *G. sp.* of Bolivia on one branch, and *G. narcissoides* and *G. magellanica* branching from a different node). This suggests a very rapid radiation in South America just prior to, and immediately following, the time of dispersal from South America to New Zealand. The position of *G. saxosa*, *G. antipoda*, *G. antarctica*, and *G. cerina* near or at this central node is, I believe, correct, and the position of *G. bellidifolia* and *G. serotina* at this node, may indicate that the *G. bellidifolia* group is sister group to the *G. saxosa* group.

A synapomorphy uniting *G. antipoda* and *G. antarctica* at position 20 in Fig. 38 reflects a similarity in morphology of those two species. Other synapomorphies exist: one unites *G. impressinervia* and *G. astonii* at position 3, one unites *G. impressinervia*, *G. astonii*, *G. montana* var. *stolonifera* and *G. bellidifolia* at position 9; one unites *G.*

impressinervia, *G. astonii* and *G. chathamica* at position 29; and one unites *G. serotina*, *G. bellidifolia*, *G. saxosa*, and *G. lineata* at position 67. Conflicts between these synapomorphies show as boxiness in the centre of the median network, and indicate that some homoplasy in the mutations exists. In my opinion, some of the relationships shown in the median network graph are untrue, e.g., the relationship shown between *G. impressinervia* and *G. astonii* which have identical sequences, the separation of *G. chathamica* and *G. spenceri* on the network, and the separation of the two samples of *G. bellidifolia*.

Leaf epidermal patterns

All six species of the *G. saxosa* group show a lack of zig-zagging in their leaf epidermal cell walls (Fig. 40). In the *G. divisa* group, *G. luteoalba* and *G. divisa* show a semi-zig-zagged state. In the *G. montana* group, *G. vernicosa* and some specimens of *G. montana* are very similar to the *G. saxosa* group in having non-zig-zagged cells that are almost square.

Photographs were taken of cuticles of other species but not analysed because the cell wall boundaries could not be traced accurately. *G. antarctica* (E. J. Godley, Venus Bog, Campbell Island) and *G. cerina* (C. Meurk, Auckland Is.) show the same non-zig-zagged pattern as *G. saxosa* and *G. concinna*. *G. antipoda* has the same lack of zig-zagging as the other species of the *G. saxosa* group, but its shape factor is low because the cells measured were elongated. *G. divisa* from Shotover Saddle is also anomalous, and its very thick cell walls may have influenced the result. Other species analysed are presented in Table 43.

Table 43 Shape factor in epidermal cells of New Zealand *Gentianella*, ordered from non-zigzagged to strongly zigzagged.

	Specimen	Shape factor $\pm 0.1-0.2$
<i>G. concinna</i>	<i>C. Meurk</i> , Auckland Is., CHR 5100017	0.6
<i>G. montana</i> var. <i>stolonifera</i>	<i>D. Glenny</i> 7357, Lookout Range, CHR 559983	0.58
<i>G. saxosa</i>	<i>D. Glenny</i> 6372, Big Bungaree Beach, CHR 509898	0.55
<i>G. saxosa</i>	<i>B. Rance</i> 2/98, Waipapa Point, CHR 526415	0.54
<i>G. divisa</i>	<i>G. Spearpoint</i> , Shotover Saddle, CHR 526417	0.53
<i>G. vernicosa</i>	<i>D. Glenny</i> 7363, Mt Owen, CHR 559989	0.52
<i>G. patula</i>	<i>D. Glenny</i> 6772, Cobb Valley, CHR 530458 ex glasshouse	0.5
<i>G. luteoalba</i>	<i>D. Glenny</i> 7361, Lookout Range, CHR 559987	0.51
<i>G. spenceri</i>	<i>D. Glenny</i> 7363, Granity Pass, CHR 559989	0.5
<i>G. amabilis</i>	<i>D. Glenny</i> 6406a, Old Man Range, CHR 509931 ex glasshouse	0.43
<i>G. spenceri</i>	<i>G. Jane</i> , Dew Lakes, CHR 516236	0.42
<i>G. bellidifolia</i>	<i>D. Glenny</i> 6406b, Old Man Range, CHR 509931, ex glasshouse	0.41
<i>G. montana</i> subsp. <i>ionostigma</i>	<i>I. Breitwieser</i> 2062, Mt Hikurangi, CHR 526397	0.41
<i>G. stellata</i>	<i>G. Jane</i> , Croisilles Harbour, CHR 516246	0.4
<i>G. filipes</i>	<i>D. Glenny</i> 7374, Mount Owen, CHR 560002	0.4
<i>G. antipoda</i>	<i>E. J. Godley</i> , Antipodes Is., CHR 549027	0.39
<i>G. montana</i> var. <i>stolonifera</i>	<i>P. Suisted</i> , Croesus Knob, CHR 516249	0.39
<i>G. bellidifolia</i>	<i>P. N. Johnson</i> 1373, Old Man Range, CHR 511801	0.38
<i>G. grisebachii</i>	<i>P. N. Johnson</i> 1407, Livingstone Mountains, CHR 515002	0.38
<i>G. chathamica</i>	<i>D. Glenny</i> 7152, Waimahana Creek, CHR 559759	0.38
<i>G. bellidifolia</i>	<i>K. Hogan</i> 1, Altimarlock, CHR 526402	0.39
<i>G. corymbifera</i> subsp. <i>gracilis</i>	<i>D. Glenny</i> 7333, Fagan Downs, CHR 560136	0.38
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	<i>D. Glenny</i> 7364, Granity Pass, CHR 559990	0.38
<i>G. astonii</i> subsp. <i>arduana</i>	<i>A. Wilton</i> , Chalk Range, CHR 516239	0.36

	Specimen	Shape factor $\pm 0.1-0.2$
<i>G. gibbsii</i>	<i>D. Glenny</i> 6355, Mt Anglem, CHR 509878	0.32
<i>G. angustifolia</i>	<i>D. Glenny</i> 7365, Granity Pass, CHR 559991	0.32
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	<i>D. Glenny</i> 6918, Trent River, CHR 559475	0.3

South American and Australian species were also sampled for epidermal cell shape (Table 44), with the aim of finding South American species that might confirm whether the *G. saxosa* group of species are basal to all other New Zealand *Gentianella* species. Six of the eight species sampled have non-zig-zagged epidermal cell walls, indicating that this may well be the ancestral state of New Zealand *Gentianella*.

Table 44 Epidermal cell shape in South American and Australian *Gentianella*.

	Specimen	Leaf epidermal cells
<i>G. weberbaueri</i>	<i>D. N. Smith et al.</i> 9630, Huascaran N.P., Peru, MO 3307963.	non-zigzagged
<i>G. androsacea</i>	<i>P. M. Jorgensen et al.</i> 832, Cordillera de las Lagunitas, Ecuador, MO 4664864.	non-zigzagged
<i>G. dianthoides</i>	<i>A. sagastegui</i> A. 8405, Challuayaco, Peru, MO 2922443.	non-zigzagged, thick-walled
<i>G. boliviana</i>	<i>J. C. Solomon & M. Moraes</i> 13462, Murillo Prov., Milluni, MO 3305338.	non-zigzagged
<i>G. corymbosa</i>	<i>H. Barclay & P. Juajibioy</i> 7417, Sierra Nevada del Cocuy, Colombia, MO 2710529.	non-zigzagged
<i>G. foliosa</i>	<i>J. D. Boeke</i> 575, Cotopaxi, Ecuador, MO 2697314.	slightly zigzagged
<i>G. nummularifolia</i>	<i>H.G. Barclay & P. Juajibioy</i> 8837, Cordillera Oriental, MO 2710534	zigzagged
<i>G. ottonis</i>	<i>O. Zollner</i> , Ortiga-Arrayan, Chile, MO 2981384.	zigzagged
<i>G. cunninghamii</i>	<i>D. Frood</i> , Victoria, Mt Buffalo, CHR 447024	zigzagged
<i>G. diemensis</i> subsp. <i>plantaginea</i>	<i>A. T. Dobson</i> , Ben Lomond, CHR 398064	zigzagged

Areas of stomatal guard cells and the stomatal gap within the guard cells were measured for the same samples as for the cuticle analysis presented in Table 42. Stomatal areas

differ in range between $114 \mu\text{m}^2$ in *G. magnifica* and $26 \mu\text{m}^2$ in *G. amabilis*, a factor of four between largest and smallest. Variation within species is low in some cases (e.g., between $110 \mu\text{m}^2$ and $112 \mu\text{m}^2$ in two samples of *G. luteoalba*) but high in others (e.g., between 37 and $85 \mu\text{m}^2$ in *G. divisa*, between 65 and $95 \mu\text{m}^2$ in *G. filipes*, and between 84 and $110 \mu\text{m}^2$ in *G. montana* var. *stolonifera*). There is little similarity in values between species of the same group (e.g., species of the *G. divisa* group have both the largest and smallest stomata) indicating that stomatal size is uninformative at this level. Two *G. divisa* relatives, *G. magnifica* and *G. luteoalba*, have the largest stomata. Species with large stomatal areas such as *G. saxosa* and *G. vernicosa* are diploid and this makes it unlikely that large stomata indicates a higher ploidy level in *G. magnifica* and *G. luteoalba*.

Leaf transverse sections

A representation of leaf transverse sections is shown in Fig. 41 and descriptions of these sections are presented below.

Gentiana amabilis Leaves moderately thick, $500 \mu\text{m}$. Midrib projecting slightly, $50 \mu\text{m}$. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 5 rows, length to width ratio of palisade cells 1.5:1. Cells next to abaxial epidermis weakly elongated parallel to epidemis.

Gentianella angustifolia Leaves thin, $290\text{--}330 \mu\text{m}$. Midrib projecting $130 \mu\text{m}$. Stomata equally dense on the two surfaces. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue weakly differentiated, cells in 2 rows, length to width ratio of palisade cells c. 1:1. Cells next to abaxial epidermis weakly elongated parallel to epidemis.

Gentianella antarctica Leaves moderately thick, $670 \mu\text{m}$. Midrib projecting slightly, $40 \mu\text{m}$, lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade

tissue weakly differentiated, cells in 2 rows, length to width ratio of palisade cells 1.4:1.

Gentianella antipoda Leaves moderately thick, 430–440 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 2–3 rows, length to width ratio of palisade cells 1.4:1.

Gentianella astonii ssp. *astonii* Leaves very thick, 1040 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue strongly differentiated, cells in 5 rows, length to width ratio of palisade cells 1.9:1. Cells next to abaxial epidermis not elongated.

Gentianella astonii ssp. *arduana* Leaves moderately thick, 580–730 μm . Midrib not projecting or projecting slightly, 30 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, cells of adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching half way or more than half way from abaxial surface. Palisade tissue absent to strongly differentiated, where differentiated, cells in 2–3 rows, length to width ratio of palisade cells 1.6:1.

Gentianella bellidifolia s. s. Leaves thin, 280–300 μm . Midrib projecting 100 μm , lateral nerves not projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis uniform in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue strongly differentiated, cells in 2 rows, length to width ratio of palisade cells 1.7:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella bellidifolia "Red Hills Peat" Leaves thin, 310–340 μm . Midrib projecting 110–150 μm , lateral nerves not projecting. Stomata equally dense on the two surfaces or denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue weakly asymmetrical, airspaces reaching

half way from abaxial surface. Palisade tissue weakly differentiated, cells in 1–2 rows, length to width ratio of palisade cells 1.3:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella cerina Leaves moderately thick or very thick, 730–840 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis uniform in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 4 rows, length to width ratio of palisade cells 1.4:1.

Gentianella chathamica Leaves moderately thick, 380–440 μm . Midrib projecting 190 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 3 rows, length to width ratio of palisade cells 1.4:1.

Gentianella concinna Leaves thin, 390 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis uniform in size. Airspaces reaching less than half way from abaxial surface. Palisade tissue absent.

Gentianella corymbifera ssp. *gracilis* Leaves moderately thick or very thick, 700–820 μm . Midrib projecting slightly, 30 μm , lateral nerves projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue absent.

Gentianella decumbens Leaves moderately thick, 500–520 μm . Midrib projecting slightly, 70–90 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue strongly differentiated, cells in 2–3 rows, length to width ratio of palisade cells 1.7:1.

Gentianella divisa Leaves moderately thick, 400–520 μm . Midrib projecting slightly, 30 μm , lateral nerves projecting. Stomata equally dense on the two surfaces. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue absent.

Gentianella filipes Leaves moderately thick, 420–440 μm . Midrib projecting slightly, 70 μm , lateral nerves not projecting. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue absent.

Gentianella gibbsii Leaves thin, 250–290 μm . Midrib projecting slightly, 20 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue absent.

Gentianella grisebachii Leaves moderately thick, 560–710 μm . Midrib projecting 160 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue strongly differentiated, cells in 3 rows, length to width ratio of palisade cells 1.7:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella lineata Leaves thin, 320–380 μm . Midrib projecting slightly, 70 μm , lateral nerves not projecting. Stomata equally dense on the two surfaces. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical or weakly asymmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 2 rows, length to width ratio of palisade cells 1.8:1.

Gentianella luteoalba Leaves moderately thick, 520–530 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial

epidermis uniform in size, adaxial epidermis uniform in size. Interior leaf tissue asymmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue weakly differentiated, length to width ratio of palisade cells c. 1:1.

Gentianella magnifica Leaves moderately thick, 590 μm . Midrib projecting, 200 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis uniform in size. Interior leaf tissue symmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue absent.

Gentianella matthewsii Leaves thin, 300–380 μm . Midrib projecting 160 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue absent. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella montana ssp. *montana* Leaves moderately thick, 440–460 μm . Midrib projecting 190 μm , lateral nerves projecting. Stomata equally dense on the two surfaces. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue weakly differentiated or strongly differentiated, cells in 1 rows, length to width ratio of palisade cells 1.6:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella montana ssp. *ionostigma* Leaves thin, 260–280 μm . Midrib projecting 150 μm , lateral nerves projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 5 rows, length to width ratio of palisade cells 1.3:1. Cells next to abaxial epidermis strongly elongated parallel to epidermis.

Gentianella montana var. *stolonifera* Leaves moderately thick, 610–650 μm . Midrib projecting 250 μm , lateral nerves projecting or not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in

size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue strongly differentiated, cells in 3 rows, length to width ratio of palisade cells 2.1:1. Cells next to abaxial epidermis not elongated.

Gentianella montana "Gault" Leaves moderately thick, 470–480 μm . Midrib projecting slightly, 60 μm , lateral nerves not projecting. Stomata equally dense on the two surfaces or denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue weakly differentiated, cells in 2 rows, length to width ratio of palisade cells 1.3:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella impressinervia Leaves moderately thick, 590–610 μm . Lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue strongly differentiated, length to width ratio of palisade cells 1.8:1.

Gentianella patula Leaves thin, 270–320 μm . Midrib projecting 180 μm , lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue symmetrical, airspaces reaching less than half way from abaxial surface. Palisade tissue absent. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella saxosa Leaves very thick, 950–1040 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis uniform in size, adaxial epidermis uniform in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue strongly differentiated, length to width ratio of palisade cells 1.7:1.

Gentianella serotina Leaves moderately thick, 630–750 μm . Midrib projecting, 110 μm , lateral nerves projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue strongly

differentiated, cells in 3 rows, length to width ratio of palisade cells 1.7:1.

Gentianella spenceri Leaves moderately thick, 650–810 μm . Midrib projecting 170 μm . Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching more than half way from abaxial surface. Palisade tissue strongly differentiated, cells in 1–2 rows, length to width ratio of palisade cells 1.8:1.

Gentianella stellata Leaves moderately thick, 650–740 μm . Midrib projecting 110–150 μm , lateral nerves not projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue strongly differentiated, cells in 4 rows, length to width ratio of palisade cells 1.7:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella tenuifolia Leaves thin, 330–650 μm . Midrib projecting 200 μm , lateral nerves projecting. Stomata denser on abaxial leaf surface. Cells of abaxial epidermis varying in size, adaxial epidermis varying in size. Interior leaf tissue asymmetrical, airspaces reaching half way from abaxial surface. Palisade tissue weakly differentiated or strongly differentiated, cells in 3–4 rows, length to width ratio of palisade cells 1.3:1. Cells next to abaxial epidermis weakly elongated parallel to epidermis.

Gentianella vernicosa Leaves thick, 670–780 μm . Midrib not projecting, lateral nerves not projecting. Stomata denser on adaxial leaf surface. Cells of abaxial epidermis uniform in size or varying in size, adaxial epidermis uniform in size. Interior leaf tissue weakly asymmetrical or asymmetrical. Palisade tissue strongly differentiated, cells in 4 rows on adaxial side of leaf, also present on abaxial side of leaf, length to width ratio of palisade cells 2.4:1.

The *G. divisa* group (*G. corymbifera*, *G. divisa*, *G. filipes*, *G. luteoalba*, and *G. magnifica*) is marked by the complete lack of palisade cells. All cells in the leaf interior are isodiametric in sectional view. *G. vernicosa* is unusual in having a palisade layer present on both sides of the leaf, and in having the most elongated palisade cells of any species. The presence or absence of palisade cells was used in the morphological data

set.

The epidermal cells in members of the *G. saxosa* group (*G. saxosa*, *G. antipoda*, *G. antarctica*, *G. cerina*, *G. concinna*) are marked by two features. Firstly, the epidermal cells are even in size, both in cell width in section and cell depth. This feature is seen in the leaf cuticle peels as a lack of zig-zagging of epidermal cell walls, but the cell depth is also uniform (compare with the unequal cell depth in *G. chathamica*). Secondly, there are large air gaps extending from the epidermis to halfway through the leaf, due to the sparseness of cells in this half of the leaf.

The leaf midvein projects in some species but not in others. The midvein does not project in the thickest leaves, particularly those of *G. astonii* subsp. *astonii*, *G. concinna*, *G. cerina*, *G. saxosa*, and *G. vernicosa*. However, some of the thinner leaved taxa, e.g., *G. gibbsii*, have a low midrib. Only in the *G. saxosa* group are the leaves always thick and the midrib not projecting.

The best quantitative characters found were leaf thickness, projection of the midvein, the number of rows of palisade cells, and the palisade cell length to width ratio. These were used for a PCA (Fig. 42 and 43 — the groups have been divided into two graphs for clarity). The component scores (Fig. 44) show the two palisade characters (number of rows of palisade cells and length to width ratio of cells) are equivalent in their effect, while leaf thickness and midrib projection are independent of each other, although leaf thickness is correlated to palisade cell presence (thicker leaves have stronger palisade cell development). Leaf width was also assessed by adding it to the PCA data set and it is strongly correlated to midrib projection (indicating that wide leaves need projecting midribs for strength), but not to leaf thickness. The PCA did not cluster species according to the species groups. I concluded that it could not be used to assign taxa whose relationships were uncertain to groups (e.g., North Island populations of *G. montana*, *G. "Gault"*, *G. "subalpina"*, and *G. "volcanic plateau"*).

Chromosome counts

A recount of the chromosomes on John Hair's slide made from the Barrier Range, Fiordland, collection of John Anderson gave a count of $2n = 18$ in more than one cell and the chromosomes were normal (Dawson & Beuzenberg 2000). All four *Gentianella* species on the Barrier Range, *G. lineata*, *G. montana*, *G. divisa*, and *G. matthewsii*, gave a count of $2n = 36$ (Dawson & Beuzenberg 2000). It must be concluded that John Hair's count was from an unusual plant rather than universally present in any species there. Abnormal low counts in *Gentianella* are recorded in the literature, with counts of $2n = 18$ made by Gadnidge et al. (1992) and Dalgaard et al. (1989). The only plausible inference from these independent and isolated records is that rarely haploid (or, in this case, more accurately, dihaploid) plants of *Gentianella* do occur in nature. These must arise from spontaneous development of an unfertilised ovule and can be predicted to be sterile, since their dihaploid condition forces recombination at meiosis between homeologous chromosome sets which have probably not paired since the origin of *Gentianella* as a genus — the whole spectrum of known chromosome counts indicates that *Gentianella* is of polyploid origin where $x_2 = 18$ (J. D. Lovis, pers. comm.).

Seed dimensions

As discussed in the Introduction, seeds of *Gentianella* are unvarying in being almost smooth, and little variation in size or shape can be seen. Seed samples of 13 species measured using an image analyser varied in length between 0.84 mm and 1.23 mm except for *G. magnifica* that had seeds much larger, with a mean length of 1.83 mm long, and more ellipsoidal with a mean length to width ratio of 1.48 ($n = 14$, all from *D. Glenny* 7451, Barefell, CHR 529216). Webb & Simpson (2001) noted that all members of the *G. astonii* group have elongated seeds, and this was confirmed by a measurement of *G. astonii* subsp. *arduana* which had seeds with a length to width ratio of 1.4 (*D. Glenny* 7487, Ward Beach, CHR 525471, $n = 19$).

Webb & Simpson (2001) note that the Subantarctic species and *G. chathamica* all have small seeds while the smallest seeds belong to *G. lineata*. This observation can be explained by the fact that *G. chathamica* and the four Subantarctic species have selfing characteristics as do other small-seeded species such as *G. lineata* (0.4–0.7 mm long), *G. gibbsii* (0.8–1.1 mm long), and *G. grisebachii* (0.6–1.1 mm long). These species all have small anthers and their flowers rarely open fully. Of the Subantarctic Island species, *G. antipoda* has the smallest seeds (0.4–0.8 mm long) and also shows the selfing syndrome most strongly with anthers only 0.75–1.0 mm long, and only 3–9

ovules per ovary.

Pollen grain surface pattern

A representation of pollen grains showing the extremes and intermediates in surface pattern between striate and reticulate types is shown in Fig. 45. A subjective ranking between 0 and 9 was made of the pollen grain surface pattern where 0 is reticulate and 9 striate. The surface pattern classification in Nilsson (1967) was simplified to one of striate, striate-reticulate, and reticulate, depending on the height of the interconnecting bridges between the lirae. A caution needs to be added that the angle of view strongly changes the perceived degree of striation. When viewed at 90° to the grain surface, the bridges between the lirae are more apparent and the surface pattern appears more reticulate, while an oblique or polar view hides the bridges and makes the surface pattern appear more striate.

The *G. saxosa* group pollen grains show the strongest degree of striation (Table 45), although *G. scopulorum* had an intermediate score of 6. In the *G. montana* group, *G. montana* grains varied from strongly striate (9 in a specimen from Mt Arthur), to striate-reticulate (7, 6, and 5 in three specimens from Otago, Westland, and the North Island respectively). The other species of this group that was sampled, *G. impressinervia*, had striate-reticulate pollen grains with an intermediate score of 6. Species of the *G. divisa* group, *G. divisa*, *G. luteoalba*, *G. filipes* and *G. corymbifera*, were consistently striate. Species of the *G. spenceri* group ranged from scores of 7 in *G. stellata* to 5 in *G. spenceri*. The reticulate pattern is seen most strongly in *G. lilliputiana*. *G. lineata* is also quite strongly reticulate, but the other two members of the *G. grisebachii* group of species are not.

Table 45 Pollen surface pattern of some New Zealand, Australian, and South American *Gentianella* species ranked subjectively by degree of striation. Specimens with a five-digit number before the collector's name are SEM photographs taken at the Palynological Laboratory at Stockholm, Sweden, and the number refers to the slide number in the collection there.

Species	Specimen	Score	Surface pattern
<i>G. antarctica</i>	24689, D. R. Given 9364, Campbell Is., CHR 284293	9	striate
<i>G. montana</i>	21407, B. V. Sneddon, Mt Arthur, WELTU 15673	9	striate
<i>G. antipoda</i>	24684, R. H. Taylor, Antipodes Is., CHR 280165	8	striate

Species	Specimen	Score	Surface pattern
<i>G. cerina</i>	24688 <i>D. J. Campbell</i> , Auckland Is., WELT 11170	8	striate
<i>G. saxosa</i>	23886, <i>W. D. Burke</i> , Waipapa Pt, WELTU 14661	8	striate
<i>G. divisa</i>	<i>D. Glenny</i> 6850, Gertrude Saddle, CHR 559414	8	striate-reticulate
<i>G. gibbsii</i>	24683, <i>H. D. Wilson</i> , Mt Anglem, CHR 355442	7	striate-reticulate
<i>G. montana</i>	<i>D. Glenny</i> 6870, Routeburn Valley, CHR 559431	7	striate-reticulate
<i>G. luteoalba</i>	<i>D. Glenny</i> 7361, Lookout Range, CHR 559987	7	striate-reticulate
<i>G. filipes</i>	<i>D. Glenny</i> 7374, Mt Owen, CHR 560002	7	striate-reticulate
<i>G. stellata</i>	<i>P. Heenan</i> , Red Hills, CHR 565234	7	striate-reticulate
<i>G. serotina</i>	24640, <i>C. J. Webb</i> , Lake Lyndon, CHR 283763	7	striate-reticulate
<i>G. concinna</i>	24687, <i>W. R. Sykes</i> , Auckland Is., CHR 437301	7	striate-reticulate
<i>G. patula</i>	<i>D. Glenny</i> 6750, Fenella Hut, CHR 559321	7	striate-reticulate
<i>G. corymbifera</i>	<i>D. Glenny</i> 6296, Culliford Hill, CHR 509815	7	striate-reticulate
<i>G. montana</i> "Gault"	<i>D. Glenny</i> 6891, Lake Gault, CHR 559452	6	striate-reticulate
<i>G. decumbens</i>	<i>I. Breitwieser</i> 2005, Round Lake, Cobb V., CHR 516222	6	striate-reticulate
<i>G. impressinervia</i>	<i>A. P. Druce</i> , Glasgow Range, CHR 394530	6	striate-reticulate
<i>G. corymbifera</i>	<i>D. Glenny</i> 6281, Lake Tennyson, CHR 509799	6	striate-reticulate
<i>G. scopulorum</i>	<i>Anon.</i> , Charleston, CHR 10972	6	striate-reticulate
<i>G. "subalpina"</i> = <i>G. grisebachii</i> ?	<i>M. Simpson</i> 905, Franz Josef, CHR 7741	6	striate-reticulate
<i>G. chathamica</i>	<i>D. Glenny</i> 7260, Chatham Is., CHR, 526291	6	striate-reticulate
<i>G. foliosa</i>	23883, <i>S. Laegaard</i> 53880, Ecuador, QCA	5	striate-reticulate
<i>G. montana</i> ssp. <i>ionostigma</i>	<i>I. Breitwieser</i> 2062, Hikurangi, CHR 516222	5	striate-reticulate
<i>G. astonii</i> ssp. <i>arduana</i>	<i>D. Glenny</i> 7487, Weld Cone, CHR 525471	5	striate-reticulate

Species	Specimen	Score	Surface pattern
<i>G. astonii</i> ssp. <i>arduana</i>	<i>G. Simpson</i> , Chalk Range, CHR 109518	5	striate-reticulate
<i>G. spenceri</i>	<i>D. Glenny</i> 6756, Fenella Hut, CHR 530439	5	striate-reticulate
<i>G. diemensis</i>	23885, <i>A. T. Dobson</i> 77124, Tasmania, CHR 314353	4	striate-reticulate
<i>G. astonii</i> ssp. <i>awahokomo</i>	<i>B. Molloy</i> , Awahokomo, CHR 529113	3	reticulate
<i>G. lineata</i>	24686, <i>P. N. Johnson</i> , Ajax Bog, CHR 364169	3	reticulate
<i>G. lilliputiana</i>	<i>A. F. Mark</i> , Lauder Creek, Dunstan Mountains, OTA 41684	0	reticulate
<i>G. lilliputiana</i>	<i>D. Bruce</i> , Lauder Creek, Dunstan Mountains, CHR 418480	0	reticulate

Ecology of New Zealand *Gentianella* species

Most New Zealand gentian species are found in the alpine zone, or at least above the treeline. Some species are found in induced open tussocklands and grasslands or tussock shrublands at montane and subalpine altitudes (e.g., *G. corymbifera* and *G. serotina*). Two species and one subspecies of forests and forest margins (*G. spenceri*, *G. tenuifolia*, and *G. chathamica* subsp. *nemorosa*). Two are coastal species (*G. saxosa* and *G. scopulorum*). *G. lineata* ranges from coastal to alpine habitats, and may be found under forest. Subantarctic island species occupy a wide range of habitats, especially *G. concinna* and *G. cerina* on the Auckland Islands, ranging from coastal turflands, low forest, short and tall tussocklands, and alpine fellfields, and occur on soils that are mostly damp and peaty, ranging from low fertility cushion bogs to soils of moderate fertility. Some species have a strong preference for poorly drained soil conditions (e.g., *G. grisebachii*) while others are found in both wet and well drained soils (e.g., *G. stellata*, *G. bellidifolia*, *G. patula*, and *G. vernicosa*). The habitat range of many of the species is narrow and is often useful in identification. Below is a summary of the major habitats of the New Zealand *Gentianella* species.

1. Coastal habitats: *Gentianella saxosa* is most commonly found on rock outcrops only c. 2 m from high tide level with *Brachyglottis rotundifolia* and *Anaphalioides hookeri*. It also occurs in sandy coastal sites under *Leptospermum scoparium* scrub. *G. scopulorum* is found on the top of coastal cliffs in turf land, grassland, and flaxland. *G. astonii* ssp. *arduana* is found on steep coastal limestone hillslopes with *Poa cita*, *Microseris scapigera*, and other herbs. Both *G. saxosa* and *G. lineata* occur in coastal cushion bog in wet peat soils, sometimes with *Donatia novae-zelandiae*. On the Auckland Islands *G. cerina* and *G. concinna* are present in the short coastal turflands composed of *Isolepis aucklandica*, *Rumex neglectus*, *Epilobium confertifolium*, *Lagenifera pumila*, and *Marchantia berteroana*. *G. antarctica* is absent from this habitat on Campbell Island.

2. Subalpine forest and scrub, open areas in forest or forest margins: *Gentianella spenceri* is mostly found under a closed forest canopy, while *G. tenuifolia*, *G. grisebachii*, *G. chathamica* subsp. *nemorosa*, *G. gibbsii*, *G. lineata*, *G. montana* subsp. *ionostigma* can be often found on forest margins or in openings in forest. Soils are well drained but often peaty. Forest types are *Nothofagus solandri* var. *cliffortioides* and *Nothofagus menziesii* forest (Wellington, Nelson, and Southland), *Metrosideros umbellata*, *Weinmannia racemosa*, *Quintinia serrata*, *Archeria traversii*, *Dracophyllum traversii*, *Dracophyllum latifolium* forest (Nelson and North Westland), and *Dracophyllum rosmarinifolium*, *Leptospermum scoparium*, *Phyllocladus alpinus* scrub (throughout the South Island). On the Auckland Islands, *G. cerina* and *G. concinna* occupy the well lit margins or open canopied sites in the low forests composed of *Dracophyllum scoparium*, *D. longifolium*, *Metrosideros umbellata*, *Pseudopanax simplex*, and *Myrsine divaricata* with *Polystichum vestitum*, *Coprosma foetidissima*, *Nertera depressa*, and *Asplenium obtusatum* below the canopy.

3. Alpine tall tussocklands and shrublands: These are composed of *Chionochloa pallens*, *C. flavescens*, and *C. rigida* on hillslopes and ridges, sometimes mixed with shrubs. *Gentianella montana* subsp. *montana* and var. *stolonifera*, *G. impressinervia*, and *G. corymbifera* are found in these tall tussocklands in Nelson, Westland and Southland, and *G. divisa* is found in tall tussocklands in Fiordland. These four species are the tallest New Zealand *Gentianella* species and the flowering heads are able to reach the level of the tussock canopy. The soils are well drained to damp and of moderate fertility. Associated species are *Aciphylla colensoi*, *A. horrida*, *Ranunculus*

lyallii, *Astelia nivicola*, *A. petriei*, *Celmisia semichordata*, *C. petiolata*, *C. armstrongii* and shrubs such as *Dracophyllum rosmarinifolium*, *Ozothamnus leptophyllus*, and *Hebe odora*. *G. bellidifolia* and *G. vernicosa* are found where tall tussocks are sparse.

4. Alpine and subalpine short grasslands and cushionfields: These are composed of *Chionochloa australis*, *Chionochloa pungens*, and *Poa colensoi* grasslands and short tussocklands. *Gentianella vernicosa*, *G. montana* var. *stolonifera*, and *G. patula* are common in *Chionochloa australis* grasslands; *G. filipes* is found in *Poa colensoi* grasslands; and *G. gibbsii* is found in *Chionochloa pungens* grasslands on Stewart Island, along with *Donatia novae-zelandiae*, *Oreobolus pectinatus*, *Astelia linearis*, and the cushion-forming *Dracophyllum politum*. On the Subantarctic Islands, *G. cerina*, *G. concinna*, *G. antarctica*, and *G. antipoda* are found in the *Chionochloa antarctica* tussocklands, and where there has been grazing and modification on Campbell Island, induced *Poa litorosa* grasslands. Associated species in these Subantarctic tussocklands are: *Anisotome latifolia*, *Coprosma cuneata*, *Polystichum vestitum*, *Bulbinella rossii*, *Uncinia hookeri*, *Poa pratensis*, *Agrostis magellanica*, *Hebe bentharii*, *Ranunculus pinguis*, *Geranium microphyllum*, *Anaphalioides bellidioides*, *Stellaria decipiens*, and species of *Epilobium*. Soils are well drained (in the South Island) or peaty (in Southland, Stewart Island, and the Subantarctic Islands). The vegetation forms short dense swards which these short gentian species are able to match in height when in flower. Associated species are *Ranunculus insignis*, *Trifolium repens*, *Rytidosperma setifolium*, *Anisotome aromatica*, *Anaphalioides bellidioides*, *Celmisia traversii*, *C. spectabilis*, and *C. discolor*.

5. Fire induced and natural montane to subalpine shrublands, shrub-tussocklands, tussocklands and grasslands on hillslopes and valley floors: *Gentianella serotina*, both subspecies of *G. corymbifera*, *G. patula*, *G. tenuifolia*, *G. stellata*, and *G. grisebachii* have occupied these largely induced montane habitats that were formerly covered in forest. Soils are mostly well drained except in associated flushes and bogs. This category includes both hillslopes with fire induced grasslands and shrublands and valley floor habitats such as river terraces, roches moutonnées, moraine, alluvial and colluvial fans which may be natural and kept free of forest by frost, or induced by burning. Moraine and outwash surfaces are the habitats of *G. corymbifera* subsp. *gracilis* and *G. tenuifolia*, although *G. tenuifolia* prefers the partially shaded habitat at the margins between forest and open valley floor grasslands. Associated species are

Chionochloa macra, *Chionochloa rigida*, *Festuca novae-zelandiae*, *Agrostis tenuis*, *Hieracium pilosella*, *Raoulia glabra*, *R. subsericea*, *Bulbinella hookeri*, and *Anthoxanthum odoratum*. Three wetland types associated with these habitats can be distinguished:

5a. Tall red tussocklands: Large leaved forms of *Gentianella bellidifolia*, *G. grisebachii*, and *G. patula* are found in these tussocklands. Soils are moist and peaty and associated species are *Chionochloa rubra*, *Schoenus pauciflorus*, *Carex gaudichaudiana*, *Hebe pauciramosa*, *Bulbinella angustifolia*, *B. hookeri*, *Uncinia rubra*, *Agrostis tenuis*, *Dactylis glomerata*, and *Craspedia*. This habitat grades into montane and subalpine turflands with many of the same species present.

5b. Short turflands and sedgeland near lakes or tarns or on river terrace treads at montane to alpine altitudes: *Gentianella grisebachii* specialises in this habitat which suits short species that like a damp and sometimes flooded soil. Associated species are *Coprosma petriei*, *Bulbinella angustifolia*, *Celmisia gracilentia*, *Helichrysum filicaule*, *Carex coriacea*, *Euphrasia zelandica*, *Breutelia pendula*, and *Polytrichum juniperinum*.

5c. Pakihi: These are induced montane shrublands dominated by *Leptospermum scoparium*, *Empodisma minus*, *Gleichenia* and *Baumea rigida*, sometimes on peat, but more often on gleyed and podzolised soils on old glacial outwash terraces, old beach surfaces, or on the impoverished granite-derived soils of the coal plateaux of Westland. Similar vegetation occurs on Chatham Island on peat soils. *Gentianella montana* var. *stolonifera*, *G. montana* subsp. *montana* (in South Westland) and *G. chathamica* occur in this habitat. Associated species are *Baumea tenax*, *Thelymitra* species and *Drosera arcturi*.

6. Scree and fellfield: *Gentianella magnifica* is found only on fine black argillite scree. *G. divisa*, *G. luteoalba*, and *G. decumbens* are found on summit or ridgeline fellfields. These species have a substantial taproot that anchors them in the sometimes unstable substrate and the three monocarpic species appear to mast to some degree. The soils are well drained, coarsely stony, with little organic matter. Associated species are *Epilobium pycnostachyum*, *Stellaria roughii*, *Lignocarpa carnosula*, *Rachelia glaria*, *Chionohebe pulvinaris*, *Haastia sinclairii*, and *Leucogenes grandiceps*. *G. bellidifolia* can be found in high altitude snow-bank sites in skeletal soils in which

Marsippospermum gracile predominates, with *Celmisia sessiliflora*, *C. laricifolia*, and *Ourisia caespitosa*. The Auckland Island and Campbell Island gentians occupy related sites in fellfields at high elevation in which *Marsippospermum gracile* and *Pleurophyllum hookeri* dominate.

7. Limestone outcrops with shrublands and grasslands of the eastern South Island at low altitudes (0-1050 m): *Gentianella astonii* and *G. calcis* are confined to such habitats. Soils are seasonally very dry and plants often grow out of pockets and cracks in the bedrock. Associated species are *Coprosma propinqua*, *Festuca rubra*, *Echium vulgare*, *Ozothamnus leptophyllus*, and *Haloragis erecta*. *G. astonii* subsp. *astonii* is the only subspecies that also grows in tussocklands with *Poa cita*.

8. Alpine herbfields and short shrublands on marble or limestone karst:

Gentianella angustifolia, *G. filipes*, and *G. corymbifera* are found in these habitats. *G. angustifolia* is usually found in shallow soils that limits the development of taller vegetation that would shade the plants. *G. filipes* is also found in this habitat, and on almost bare marble talus. Associated species are *Ranunculus lyallii*, *Hebe pinguifolia*, *Coprosma propinqua*, and *Aciphylla ferox*.

9. Alpine bogs and flushes: *Gentianella amabilis*, *G. bellidifolia*, *G. grisebachii*, *G. filipes*, *G. lilliputiana*, *G. vernicosa*, *G. corymbifera*, *G. patula*, and *G. lineata* occur in these habitats. Soils are oligotrophic and moist to wet and are usually composed of peat. Associated species of bogs are *Chionochloa rubra*, *Carex gaudichaudiana*, *C. echinata*, *Sphagnum cristatum*, *Oreobolus pectinatus*, *O. pusillus*, *O. strictus*, *Centrolepis ciliata*, *Psychrophila obtusa*, *Plantago raoulii*, *P. uniflora*, *Celmisia glandulosa*, *Carpha alpina*, *Donatia novae-zelandiae*, *Drosera arcturi*, *Euphrasia zelandica*, *Celmisia gracilentia*, *Lepidothamnus laxifolius*, *Halocarpus bidwillii*, *Hebe odora*, *H. venustula*, *Campylopus clavatus*, and *Polytrichum commune*. In flushes on sloping ground through alpine tussocklands associated species are *Dolichoglottis lyallii*, *Schoenus pauciflorus*, *Marsippospermum gracile*, *Poa kirkii*, and *Craspedia* species.

Floral biology and breeding systems

Protandrous dichogamy is universal in the New Zealand species except in *G. chathamica* subsp. *chathamica* (Webb & Pearson 1993). In other species, the stigma is closed at anthesis and is below the anthers. When the stigma opens the ovary has elongated to the

point where the stigma is beyond the anthers, and the anthers have dispersed most of their pollen. In a few species (e.g., *G. stellata*), the anthers arch back to the point where they are in the sinus between the corolla lobes. In three species, *G. chathamica*, *G. lineata*, and *G. gibbsii*, anthers were observed to be introrse during the female phase, and selfing may be the main method of pollination. Whether the anthers invert in the four Subantarctic species is unknown. In many species the flowers in female phase have the anthers close to the stigma, even though they may be retrorse. In these cases, selfing may also occur.

Selfing is also probably indicated by small flower parts: small anthers, a short corolla, and a poorly developed nectary that is close to the corolla base. Species with anthers less than 1 mm long are *G. lilliputiana*, *G. lineata*, *G. filipes*, *G. antipoda*, *G. cerina*, *G. concinna*, *G. chathamica* (ssp. *chathamica* and ssp. *nemorosa*), and small forms of *G. grisebachii*. These species have corollae less than 9 mm long. However, of these eight species, five have coloured corolla veins (sometimes or always), and *G. concinna* and *G. cerina* have, at times, very strong coloration in the flowers. The largest corollae and anthers are found in the *G. bellidifolia* group of species, which have no colour in the corolla (with the exception of North Island *G. bellidifolia* populations). Thus, the association of guide marks in the corolla with outcrossing and its reverse is not observed in *Gentianella* as it is in *Parahebe* (Garnock-Jones 1976).

The opening of the corolla is responsive to weather conditions in most species. Flowers of most species open wide in full sunlight, closing at night and in dull or wet conditions. However, a few species with small flowers (e.g., *G. grisebachii*) can be seen shut in full sunshine, but it may be that these have already been pollinated.

Pollinators seen to visit the flowers were native bees (*Hylaeus* and *Lasioglossum*), introduced honey bees (*Apis mellifera* – even in remote alpine areas such as the Marino Mountains), introduced bumble bees (also in the alpine zone); flies of families Syrphidae, Tachinidae, Muscidae and Calliphoridae; the tussock ringlet butterfly (*Argyrophenga antipodum*) and white butterfly (*Pieris rapae*). Beetles and thrips appear to feed on nectar and pollen, and beetles may chew on other flower parts. Ovaries are often consumed by caterpillars when specimens are collected and kept before drying. In alpine areas, it is possible to see open receptive flowers with almost no pollinators present all day, while at other times, one or two species of syrphid or bee will be working the flowers in an area very systematically. For native bees and syrphids, the pollen is deposited on the back of the insect when it crawls down the corolla lobe toward the nectary. Pollinators were seen in large numbers on *G. corymbifera* and *G. amabilis*.

Male sterility in the form of non-functional or absent anthers or stamens, has been recorded for eight species: *G. antipoda* (Godley 1982, p. 413), *G. bellidifolia* (Burrows & Hobbs 1964 and pers. obs.), *G. astonii*, *G. spenceri*, *G. divisa* (Simpson & Webb 1980), *G. decumbens* (A. P. Druce, Matiri Plateau, CHR 354903), *G. filipes*, *G. montana*, *G. impressinervia*, and *G. corymbifera* (pers. obs.). It occurs sporadically and is not a constant feature of any species, and since it is rarely the case that all flowers on a plant are female, does not usually amount to gynodioecy. Hobbs & Burrows (1964) noted that female flowers of *G. bellidifolia* were smaller than hermaphrodite flowers and this is the case in other species. *G. corymbifera* on Mt Stokes (*Breitwieser 2110* & A. Wilton, CHR 526396) had small female flowers only 11 mm long (normal flowers are c. 17 mm long). *G. filipes* from Horseshoe Basin on Mt Arthur (*D. Glenny 7441*, CHR 560069) had 3 female flowers out of 14 flowers and they were smaller (7.3–7.8 mm, instead of 10.0–12.0 mm long). The female flowers were not at the base of the plant. A specimen of *G. filipes* from the Garibaldi Range (*D. Glenny 7421*, CHR 560052) had a single female flower 7.0 mm long on a plant with 20 hermaphrodite flowers. A separate collection of *G. filipes* also from the Garibaldi Range (*K. Ford 61/98*, CHR 510620) had one female flower 6.5 mm long and one flower with rudimentary anthers on a plant with six normal flowers. Male sterility was also observed in the unusual Kelly Range population of *G. montana* where all plants had a high proportion of female flowers (*D. Glenny 6464*, CHR 509989). A specimen of *G. corymbifera* (*D. Glenny 7436*, Balloon Hut, CHR 560065) had female flowers low on the flowering stems. Webb & Littleton (1986) noted male sterility in *G. astonii* s. s., and it also occurs in *G. astonii* subsp. *arduana* (*D. Glenny 7488*, CHR 525472). Plants of *G. divisa* at Lake Wapiti, Fiordland (*D. Glenny 7476*, CHR 560103) in April had only female flowers, a rare case of gynodioecy in a population.

Male sterility in some cases is a late-season phenomenon and may serve the function of using limited resources only on the female function. This might be expected in monocarpic species, and examples of this are *G. filipes*, *G. corymbifera*, *G. divisa*, *G. spenceri*, and *G. antipoda*. However, it also occurs in polycarpic species such as *G. bellidifolia*, both subspecies of *G. astonii*, *G. impressinervia*, *G. decumbens*, and *G. montana*, and may be seen at the height of the flowering season. Dioecy is particularly common in the New Zealand flora and, in non-fleshy fruited species, may result from selection pressure against self-fertilisation in non-specialised flowers (Lloyd 1985). Such selection pressure in the direction of dioecy may be responsible for male sterility in the gentians. Male sterility was noted by Gillett (1957) in the North American species

Gentianella microcalyx. Gillett says in his description of this species "flowers perfect, occasionally unisexual by abortion of the anthers (or, more rarely, the pistil)" and uses the character as one that separates this species from *G. quinquefolia*.

Hybrids

Extensive sampling of fresh specimens showed that pollen in all species is almost universally 100% stainable. A number of putative hybrid collections are present in CHR and these were tested for pollen stainability using Alexander's differential stain.

A specimen of *G. bellidifolia* × *G. lilliputiana* collected by D. Bruce (Dunstan Mountains, CHR461350 det. D. Bruce), had 8.9% ($n = 182$) of pollen unstainable and malformed. This collection has single lateral flowering stems and pigmented leaf margins and stems that are suggestive of *G. amabilis*.

A collection determined as *G. divisa* × *G. serotina* (A. P. Druce 1400, Kea Basin, Mt Earnslaw, collected at a site which had both parents present, det. A. P. Druce) had 3.7% of pollen unstainable and malformed ($n = 386$). A collection I determined as a hybrid of *G. divisa* × *G. serotina*, J. Talbot, Rock and Pillar Range, OTA 37795, had only 1.0 % ($n = 294$) of pollen malformed and unstainable. *G. serotina* is present on the sheets of both of these collections but there are also hybrids of this and *G. divisa* on the same sheets with filaments only 1.5 mm wide and a petiole width of 5.2 mm, a combination of features that suggests a hybrid. Other specimens from the Rock and Pillar Range are undoubtedly *G. divisa*, for instance A. F. Mark, Rock and Pillar Range, 4500 ft (OTA 21733) with the note "A variable population" but this specimen has pollen that is 100% stainable, while an intermediate plant on sheet OTA 37795 has 99.0% stainable pollen.

Two collections, A. P. Druce, near Anderson's Hut, Tararua Range, CHR 190614 and A. P. Druce, Whana Huia Range, CHR 165851–165854, were determined by Druce as *G. patula* × "rimutaka" hybrids, i.e., *G. grisebachii* × *G. montana* subsp. *ionostigma*. The Anderson's Hut specimen had 60% ($n = 121$) of pollen grains unstainable and misshapen by being elliptical rather than spherical, confirming Druce's identification of these plants as hybrids. Pollen sampled from two plants from Druce's Whana Huia Range mass collection was 100% fully formed and stainable and in my opinion, the collection represents a mixture of the two species without hybrids. Druce apparently interpreted reduced anthers on short filaments in this collection as resulting from hybridisation, but male sterility of some flowers is the more likely cause.

Some of the specimens discussed above are hybrids as shown by both unstainable or malformed pollen grains in combination with intermediacy in morphological traits. It is difficult to detect hybrids in the field and the Talbot Rock and

Pillar Range collection indicates they cannot always be detected by examination of their pollen.

Hybridisation between species or subspecies that have been brought into contact by habitat disturbance may account for some taxonomic problems. *G. serotina* and *G. bellidifolia* may be hybridising on the Central Otago ranges and in parts of Southland, giving rise to difficulties in separating these two there. Hybridisation of *G. vernicosa* and *G. montana* s. l. may be the origin of *G. montana* var. *stolonifera*, and may account for the unusual variation within *G. montana* var. *stolonifera*.

Flowering time

Table 46 tabulates the flowering times of the New Zealand species. Earliest flowering times are recorded for *G. chathamica* in August and September which I take to be early rather than late because flowering plants have also been collected in November. Species that flower in December are all the members of the *G. saxosa* group, *G. amabilis*, *G. lineata*, *G. spenceri*, *G. patula*, and *G. corymbifera* in the valley floors. The latest flowering species are all subspecies of *G. astonii* which are still flowering in May. Species that commonly flower in April are *G. vernicosa*, *G. serotina*, and *G. stellata*. Flowering within populations of most alpine species usually takes place over two or three weeks, but some species, particularly members of the *G. spenceri* group have a long tail to their flowering time by producing small flowers on small flowering stems at the base of the plant. The longest flowering periods are three months long and occur in *G. antipoda*, *G. concinna*, *G. gibbsii*, *G. grisebachii*, *G. filipes*, *G. montana* ssp. *stolonifera*, *G. astonii* ssp. *arduana*, and *G. chathamica* ssp. *nemorosa*.

Table 46 Flowering times in New Zealand *Gentianella* taxa, ordered from earliest to latest. Months are given in numerical form.

	Flowering months
<i>G. saxosa</i>	late 12 – early 2
<i>G. scopulorum</i>	12
<i>G. cerina</i>	(12-)1-3(-4)
<i>G. concinna</i>	11-2(-4)
<i>G. antarctica</i>	(12-)1-2(-4)
<i>G. antipoda</i>	12-3(-4)
<i>G. montana</i> ssp. <i>montana</i>	mid 1 – 3
<i>G. montana</i> ssp. <i>ionostigma</i>	1-2

	Flowering months
<i>G. montana</i> var. <i>stolonifera</i>	(1-)2-4
<i>G. patula</i>	12-1
<i>G. impressinervia</i>	2-3
<i>G. vernicosa</i>	(2-)4
<i>G. divisa</i>	1-3
<i>G. corymbifera</i> ssp. <i>corymbifera</i>	12-1 (valleys) 2-3 (alpine)
<i>G. corymbifera</i> ssp. <i>gracilis</i>	late 12-3
<i>G. filipes</i>	1-4
<i>G. luteoalba</i>	2-3
<i>G. magnifica</i>	3
<i>G. spenceri</i>	1-2(-3)
<i>G. tenuifolia</i>	1-2(-4)
<i>G. stellata</i>	3-4(-8)
<i>G. chathamica</i> ssp. <i>chathamica</i>	(8-)9-2
<i>G. chathamica</i> ssp. <i>nemorosa</i>	1-4
<i>G. grisebachii</i>	1-3
<i>G. lineata</i>	mid 11-1
<i>G. gibbsii</i>	1-3
<i>G. bellidifolia</i>	(2-)3-4
<i>G. amabilis</i>	late 12 – late 2
<i>G. decumbens</i>	1-early 3
<i>G. angustifolia</i>	2
<i>G. serotina</i>	2-4
<i>G. astonii</i> ssp. <i>astonii</i>	3-4(-5)
<i>G. astonii</i> ssp. <i>arduana</i>	3-6(-10)
<i>G. calcis</i> ssp. <i>waipara</i>	3-4
<i>G. calcis</i> ssp. <i>manahune</i>	5
<i>G. calcis</i> ssp. <i>taiko</i>	4-5
<i>G. calcis</i> ssp. <i>calcis</i>	4-5

Australian *Gentianella* species have an identical average flowering time of early February (estimated from the 40 New Zealand taxa and 19 Australian taxa in Adams

1995). Some early species flower in November and December such as the forest gentian, *G. polysperes*. Most of the species flower in January to March, and *G. nemorosa* flowers late, in March and April.

Times of North American *Gentianella*, *Gentianopsis*, and *Comastomum* species are on average three weeks later than New Zealand species of *Gentianella*, being at the start of September (estimated from 24 taxa in Gillett 1957). This corresponds to the start of March in the Southern Hemisphere.

Geographical range of species

Distributions for each species and subspecies accompany the descriptions of the species, and are derived from herbarium specimens at AK, WELT and CHR.

The centre of diversity is Nelson province, with 15 species (Fig. 46). Westland has ten species in each of two squares and the Haast area has nine. Coastal Southland and Stewart Island have eight species each. The North Island is lowest in diversity with only four species. Low North Island diversity is probably the result of the paucity of alpine habitat for a mostly alpine genus, but the genus’ absence from Taranaki indicates that dispersal is slow.

The ranges of all taxa that are not limited in their distribution by being confined to islands is given in Table 47. The most widespread species are ones which show strong morphological variation.

Table 47 Geographical range in kilometres on the longest axis, sorted from most to least widespread.

	Range (km)
<i>G. bellidifolia</i>	1360
<i>G. grisebachii</i>	1360
<i>G. montana s. l.</i>	1360
<i>G. corymbifera</i>	730
<i>G. divisa</i>	570
<i>G. serotina</i>	460
<i>G. montana</i> ssp. <i>ionostigma</i>	430
<i>G. saxosa</i>	340
<i>G. lineata</i>	300
<i>G. tenuifolia</i>	290

	Range (km)
<i>G. spenceri</i>	280
<i>G. chathamica</i> ssp. <i>nemorosa</i>	270
<i>G. stellata</i>	204
<i>G. amabilis</i>	200
<i>G. patula</i>	130
<i>G. impressinervia</i>	120
<i>G. filipes</i>	110
<i>G. montana</i> var. <i>stolonifera</i>	110
<i>G. lilliputiana</i>	100
<i>G. vernicosa</i>	100
<i>G. astonii</i> ssp. <i>arduana</i>	104
<i>G. decumbens</i>	75
<i>G. magnifica</i>	52
<i>G. angustifolia</i>	37
<i>G. calcis</i> ssp. <i>waipara</i>	28
<i>G. gibbsii</i>	c. 15
<i>G. astonii</i> ssp. <i>astonii</i>	5
<i>G. luteoalba</i>	c. 2

In addition to these, some species and subspecies have a sub-kilometre range. They are: *G. calcis* ssp. *calcis*, *G. calcis* ssp. *taiko*, *G. calcis* ssp. *manahune*, and *G. scopulorum*. Five island taxa are restricted by the size of the islands they occupy: *G. cerina*, *G. concinna*, *G. antipoda*, *G. antarctica*, and *G. chathamica* ssp. *chathamica*.

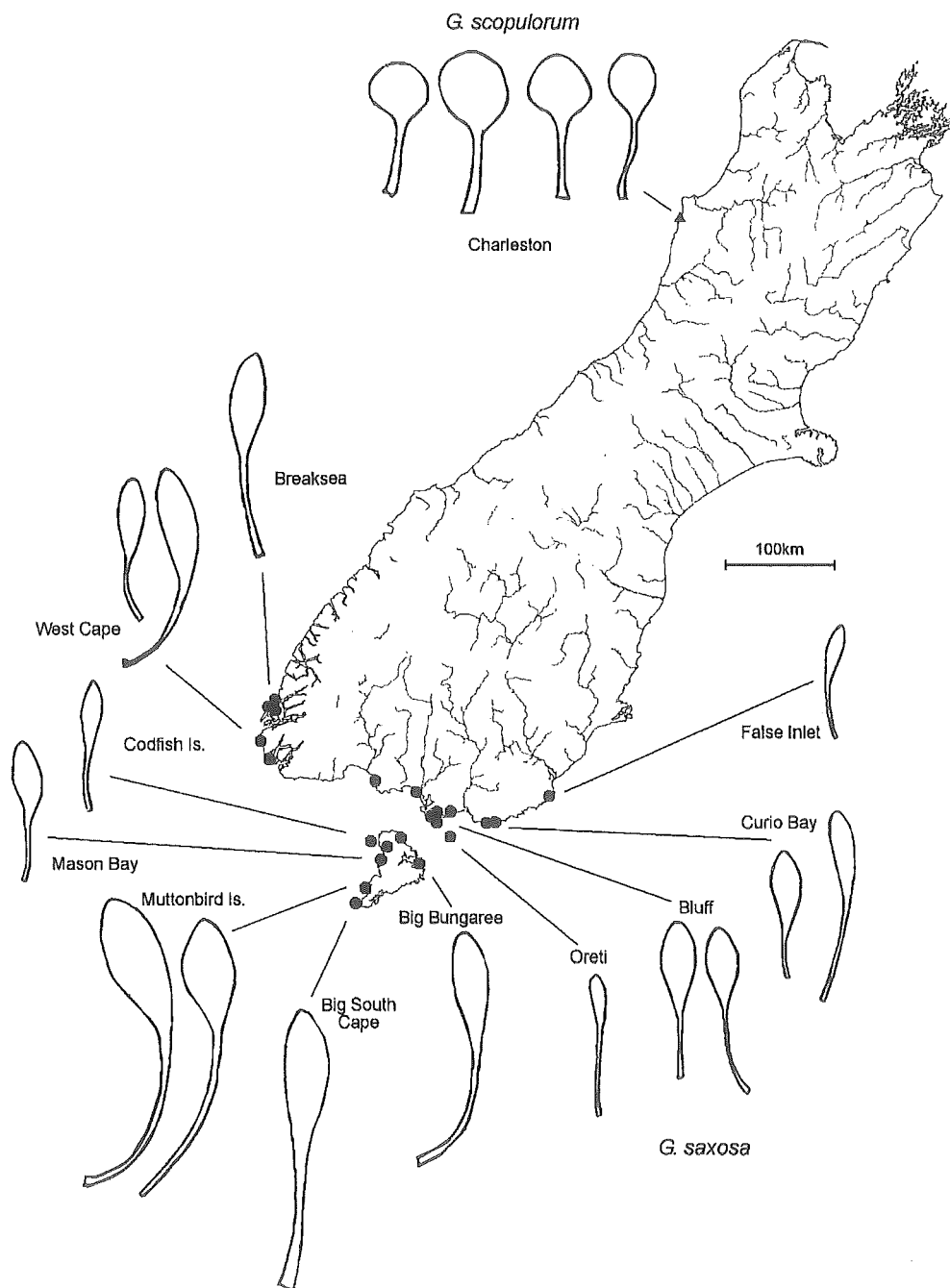


Fig. 9 Distribution and leaf silhouettes of *Gentianella saxosa* and *G. scopulorum*.
G. scopulorum: Charleston: D. Glenny 6326, CHR 509848; *G. saxosa*: Breaksea: P. N. Johnson, CHR 261516; West Cape: P. K. Dorizac, CHR 183408; Codfish Is.: I. M. Ritchie, CHR 180204; Mason Bay: J. F. Findlay, CHR 78044; Muttonbird Is.: I. M. Ritchie, CHR 401445; Big South Cape: B. Bell, CHR 115337; Big Bungaree: D. Glenny 6372, CHR 509898; Oreti: S. G. Royds, CHR 191761; Bluff: D. M. Post, CHR 201930; Curio Bay: C. J. Webb, CHR 283978; False Inlet: P. N. Johnson, CHR 494684.

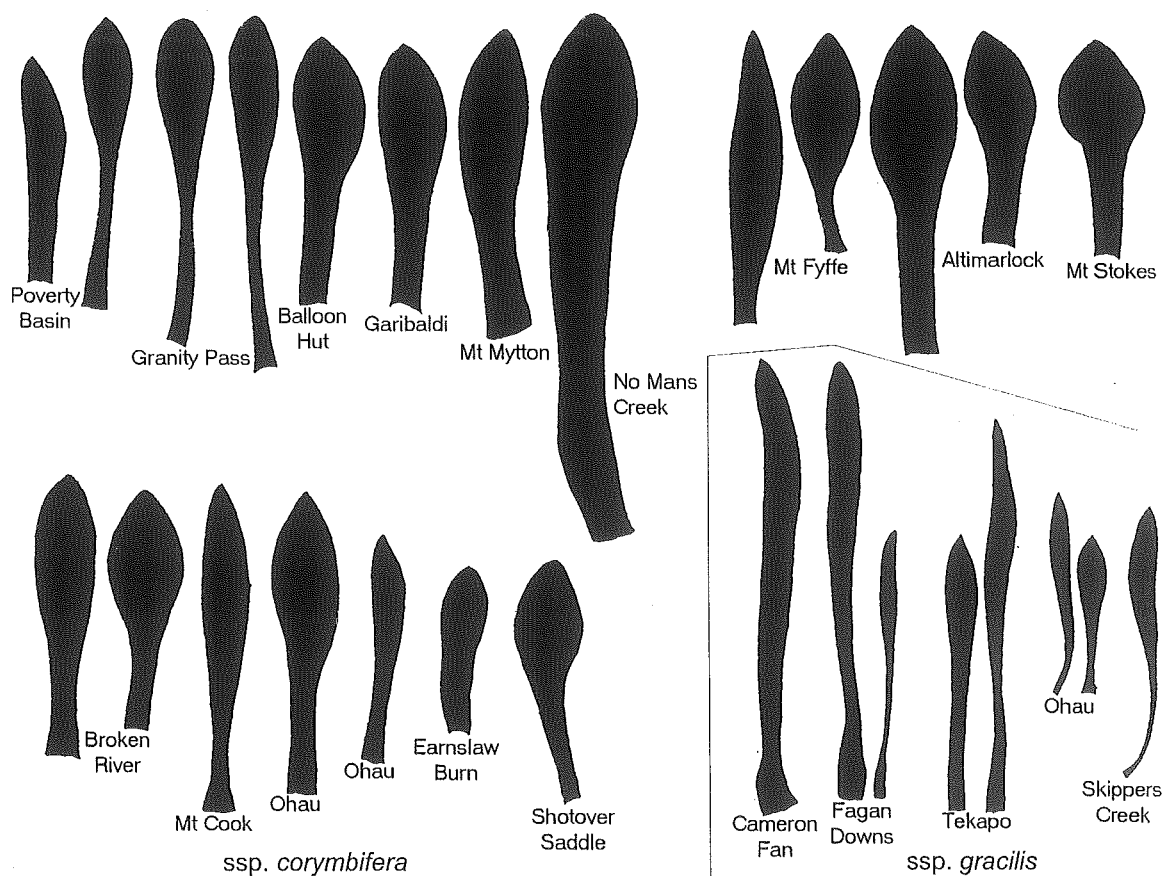


Fig. 10 Leaf silhouettes of *Gentianella corymbifera* ssp. *corymbifera* and ssp. *gracilis*.

G. corymbifera ssp. *corymbifera*: Poverty Basin: D. Glenny 7375, CHR 560001; Granity Pass: D. Glenny 7364, CHR 559990; Balloon Hut: D. Glenny 7436, CHR 560065; Garibaldi: A. Wilton & K. Ford 67/98, CHR 513665; Mt Mytton: D. Glenny 6823, CHR 530497; No Mans Creek: D. Glenny 6897, CHR 530570; Mt Fyffe: D. Huson, CHR 526403; Altimarlock: D. Glenny 7784, CHR 525274 and K. Hogan 2, CHR 526401; Mt Stokes: I. Breitwieser 2110 & A. Wilton, CHR 526396; Broken River: D. Glenny 6903, CHR 559461; Mt Cook: D. Banks, CHR 487014; Ohau: N. Simpson, CHR 526299; Earnslaw Burn: K. Wardle, CHR 526449; Shotover Saddle: G. Spearpoint, CHR 526416. *G. corymbifera* ssp. *gracilis*: Cameron Fan: D. Glenny 7335, CHR 560138; Fagan Downs: D. Glenny 7333, CHR 560136; Tekapo: P. N. Johnson 1423, CHR 518390; Ohau: D. Glenny 7354, CHR 560154; Skippers Creek: D. Glenny 6401, CHR 509926.

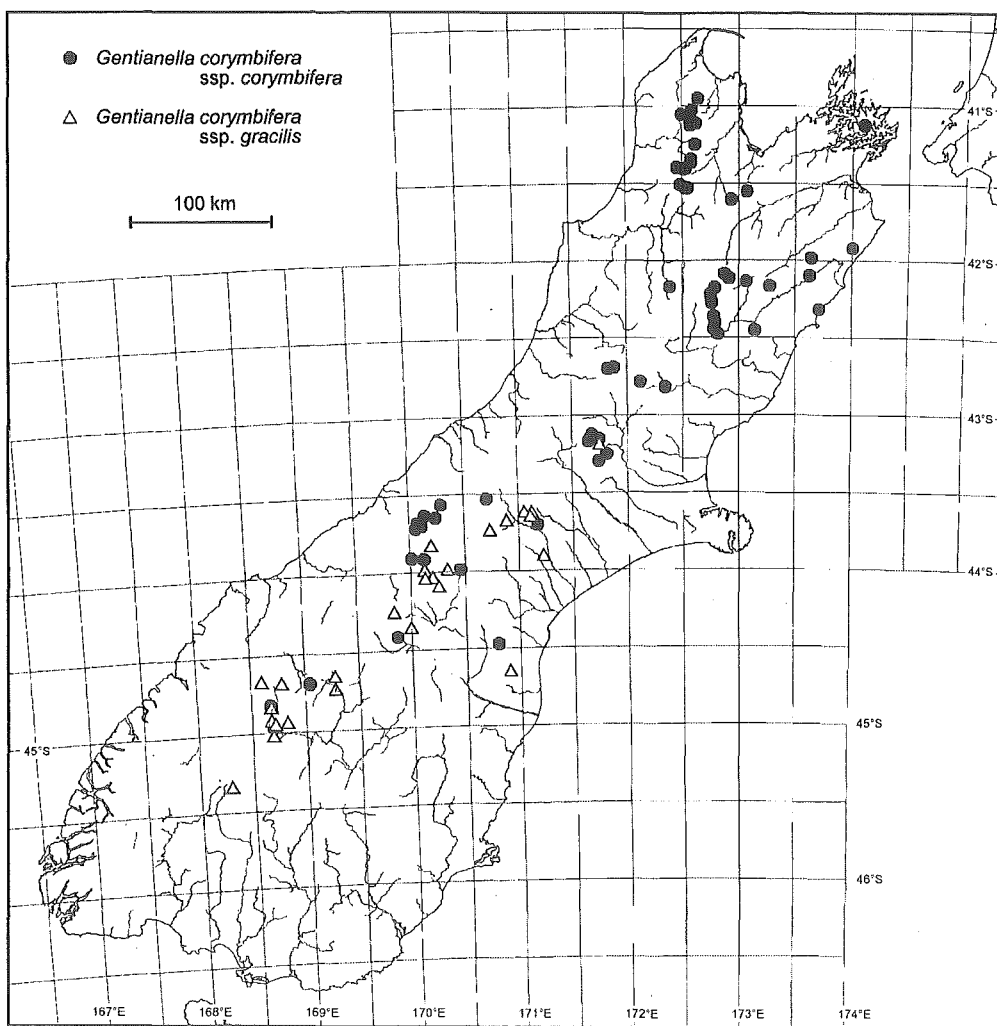


Fig. 11 Distribution of *Gentianella corymbifera*.

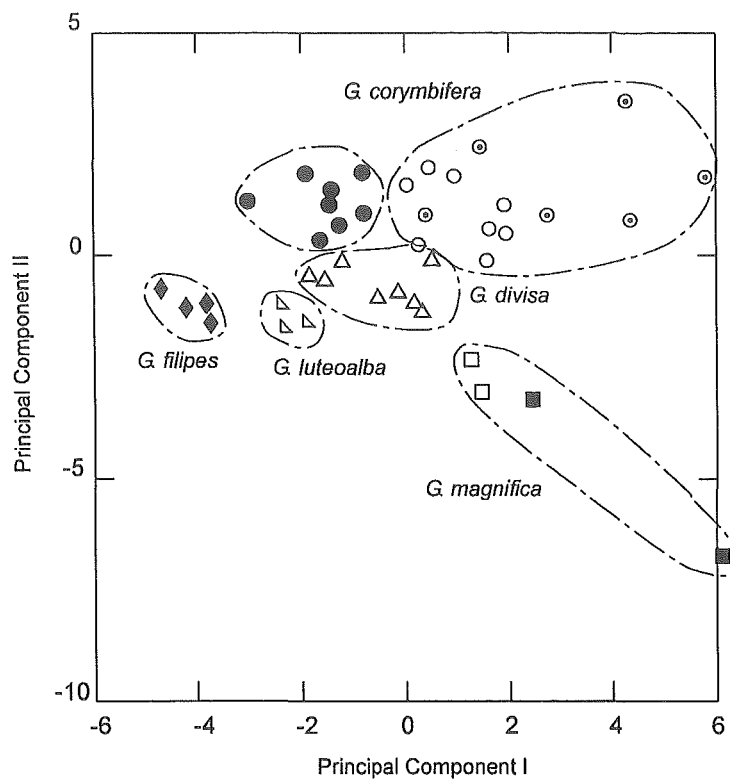


Fig. 12. Principal components analysis of *Gentianella divisa* group, principal components I and II. Principal component I explained 44% of the variance and principal component II 24%. ◆ = *G. filipes*, ▽ = *G. luteoalba* (*Gentiana* "Lookout"), △ = *G. divisa*, ● = narrow-leaved form of *G. corymbifera*, ○ = *G. corymbifera*, ⊙ = *G. corymbifera* from Nelson, ■ = *G. magnifica* (*Gentiana* "Barefell"), □ = *G. divisa* var. *magnifica*.

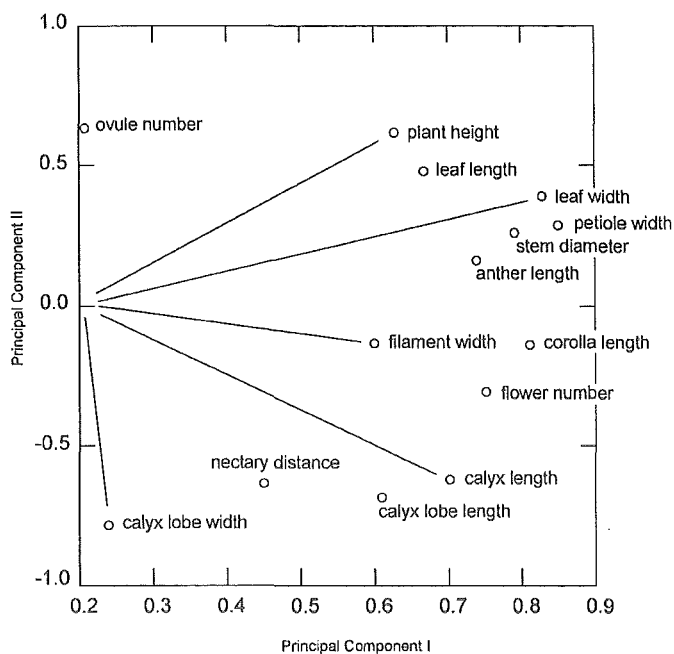


Fig. 13 Component scores for characters used in the *Gentianella divisa* group PCA, components I and II.

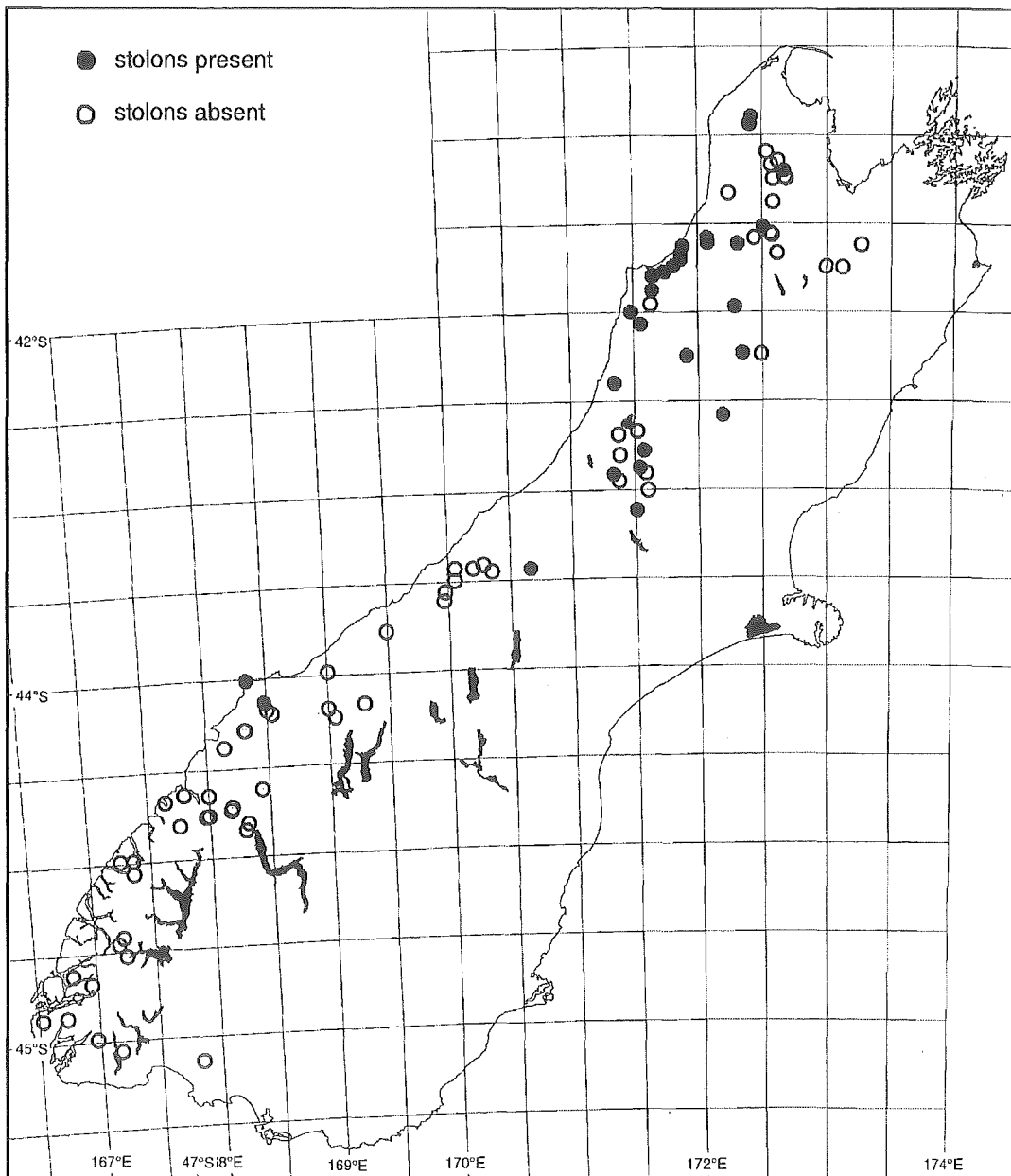


Fig. 14 Distribution of stoloniferous forms of *Gentianella montana*.

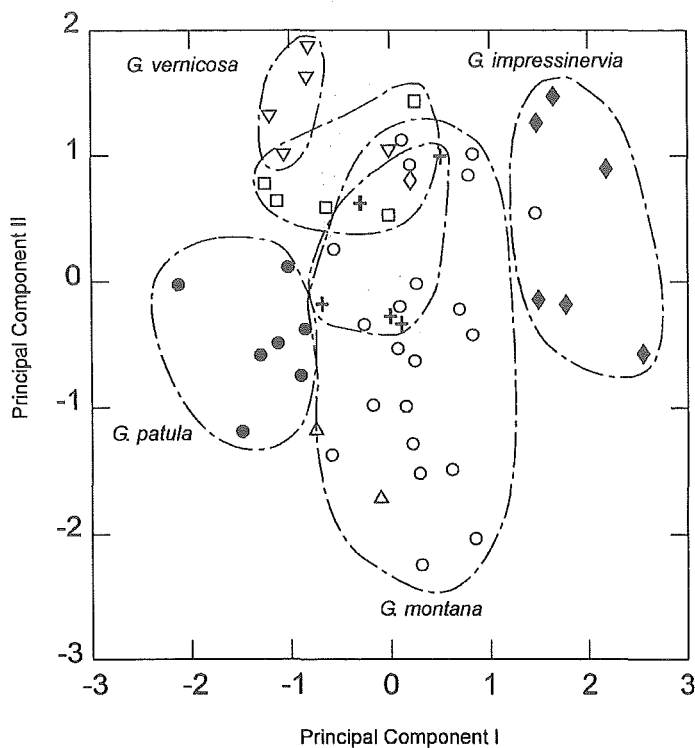


Fig. 15 Principal components analysis of the *G. montana* group, components I and II. ∇ = *G. vernicosa*, \blacklozenge = *G. impressinervia*, \square = North Island *G. montana*, $+$ = *G. montana* var. *stolonifera*, \bullet = *G. patula* (the Cobb gentian), \circ = *G. montana* s. s., \triangle = *Gentiana* "Gault".

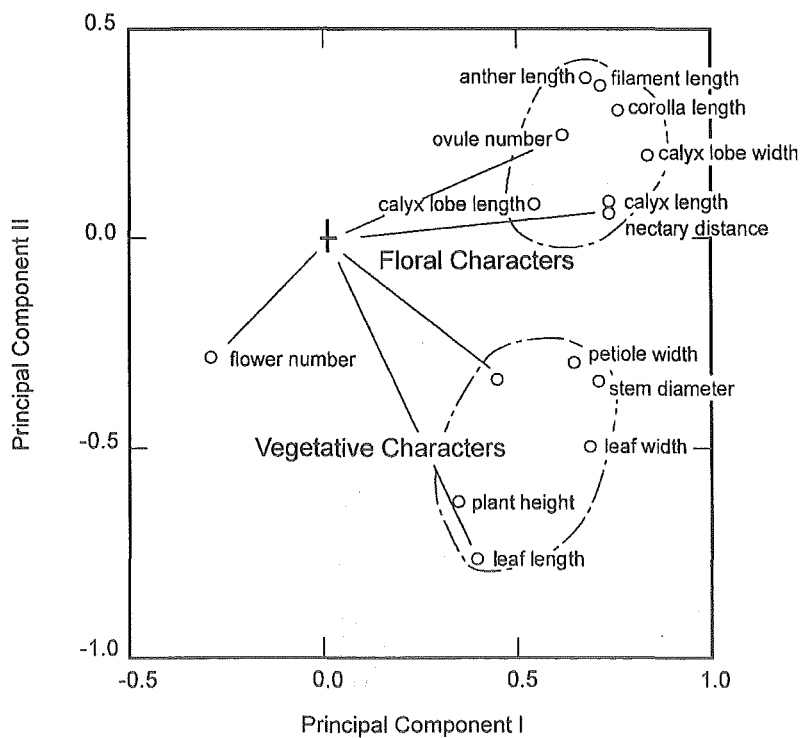


Fig. 16 Component scores for characters used in the *Gentianella montana* group PCA, components I and II.

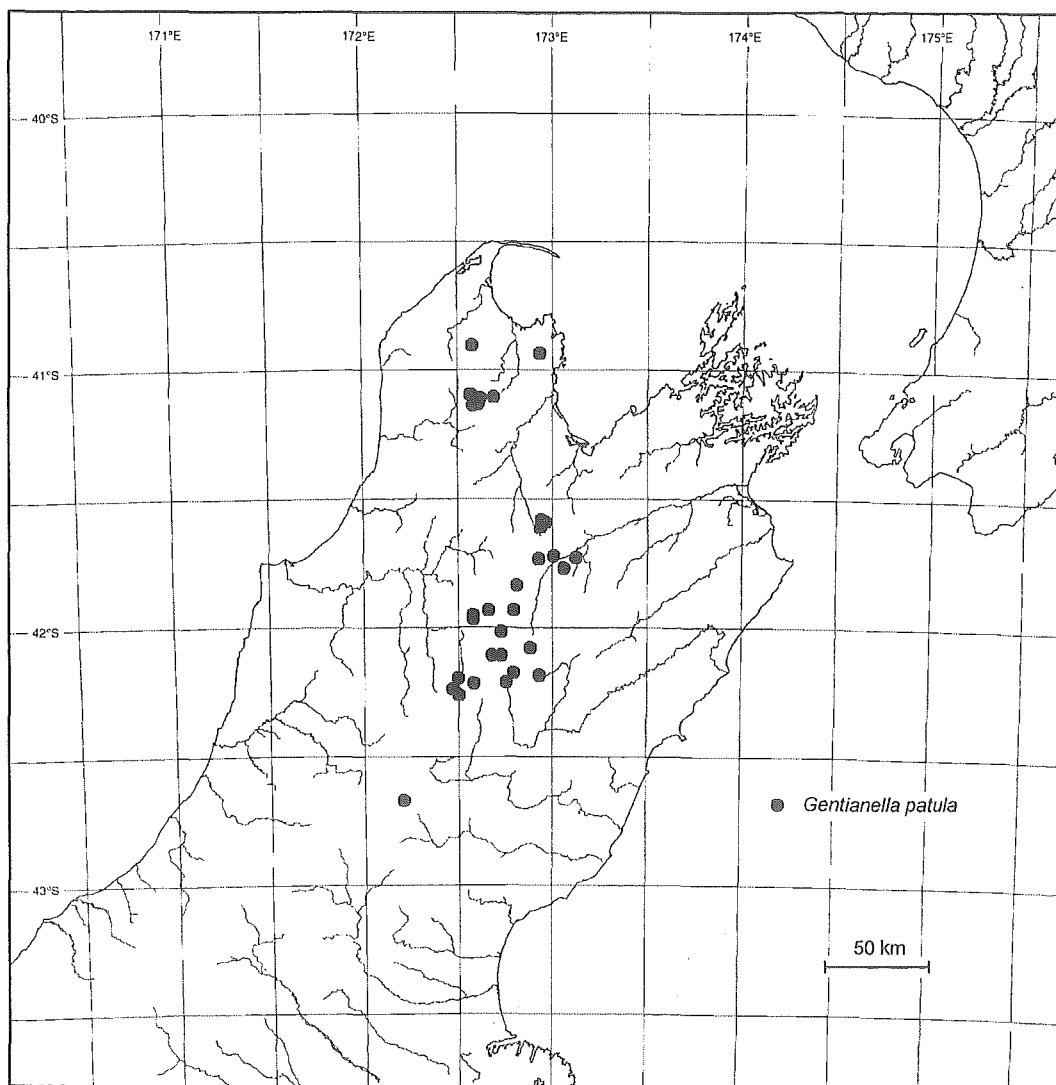


Fig. 17 Distribution of *Gentianella patula*.

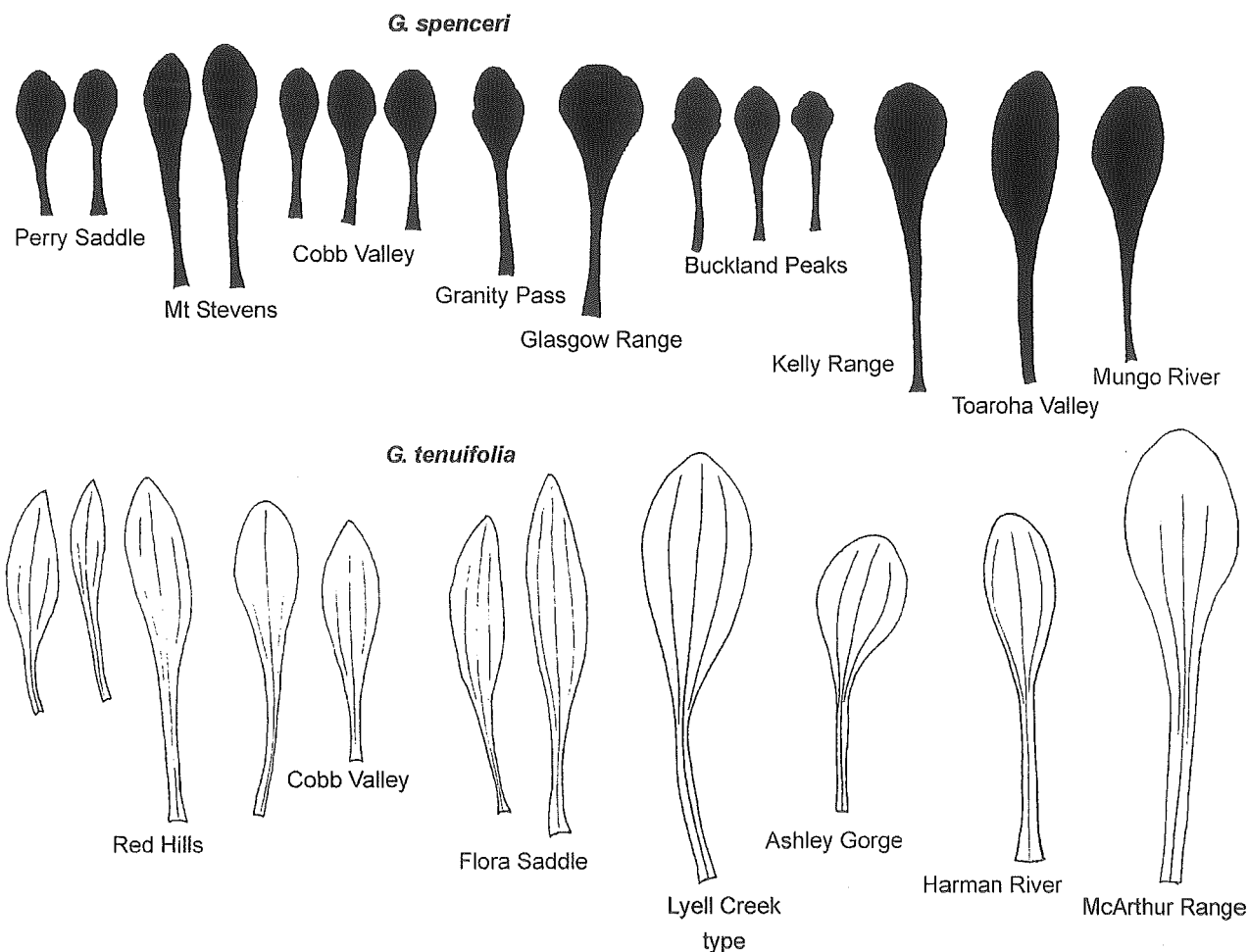


Fig. 18 Leaf silhouettes of *Gentianella spenceri* and *G. tenuifolia*.

G. spenceri: Perry Saddle: *D. Glenny* 6810, CHR 530484; Mt Stevens: *G. Jane*, CHR 526405; Cobb Valley: *D. Glenny* 6756, CHR 530439; Granity Pass: *D. Glenny* 7363, CHR 559989; Glasgow Range: *D. Glenny* 8486, CHR 526389; Buckland Peaks: *D. Glenny* 6440, CHR 509967; Kelly Range: *D. Glenny* 8492, CHR 546093; Toaroa Valley: *D. Glenny* 6949, CHR 559449; Mungo River: *D. Glenny* 6951; CHR 559501. *G. tenuifolia*: Red Hills: *D. Glenny* 6431, CHR 509958; Red Hills: *D. Glenny* 6776, CHR 530457; Cobb Valley: *D. Glenny* 6824, CHR 530498; Flora Saddle: *S. Courtney*, CHR 516225; type, Lyell Creek: *W. Townson*, WELT 4721; Ashley Gorge: *C. J. Burrows*, CHR 520188; Harman River: *D. Glenny* 6930, CHR 559484; McArthur Range: *P. Knightbridge*, CHR 526438.

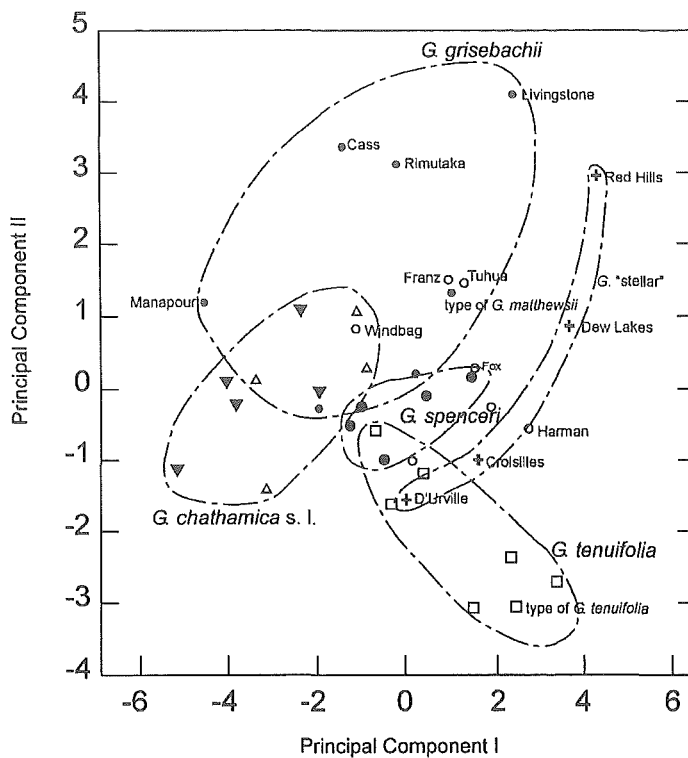


Fig. 19 Principal components analysis of the *Gentianella spenceri* group, components I and II.

▼ = *G. chathamica* ssp. *chathamica*, △ = *G. chathamica* ssp. *nemorosa* (*G.* "volcanic plateau"), + = *G. stellata* (*Gentiana* "stellar"), □ = *G. spenceri*, ○ = *Gentiana* "subalpina", ● = *G. grisebachii*.

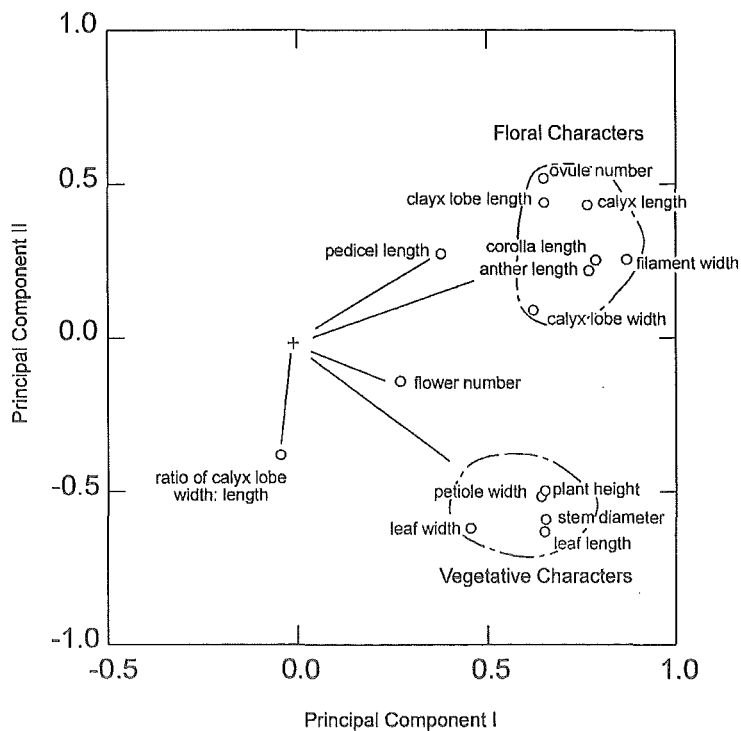


Fig. 20 Component scores for characters used in the *Gentianella spenceri* group PCA, components I and II.

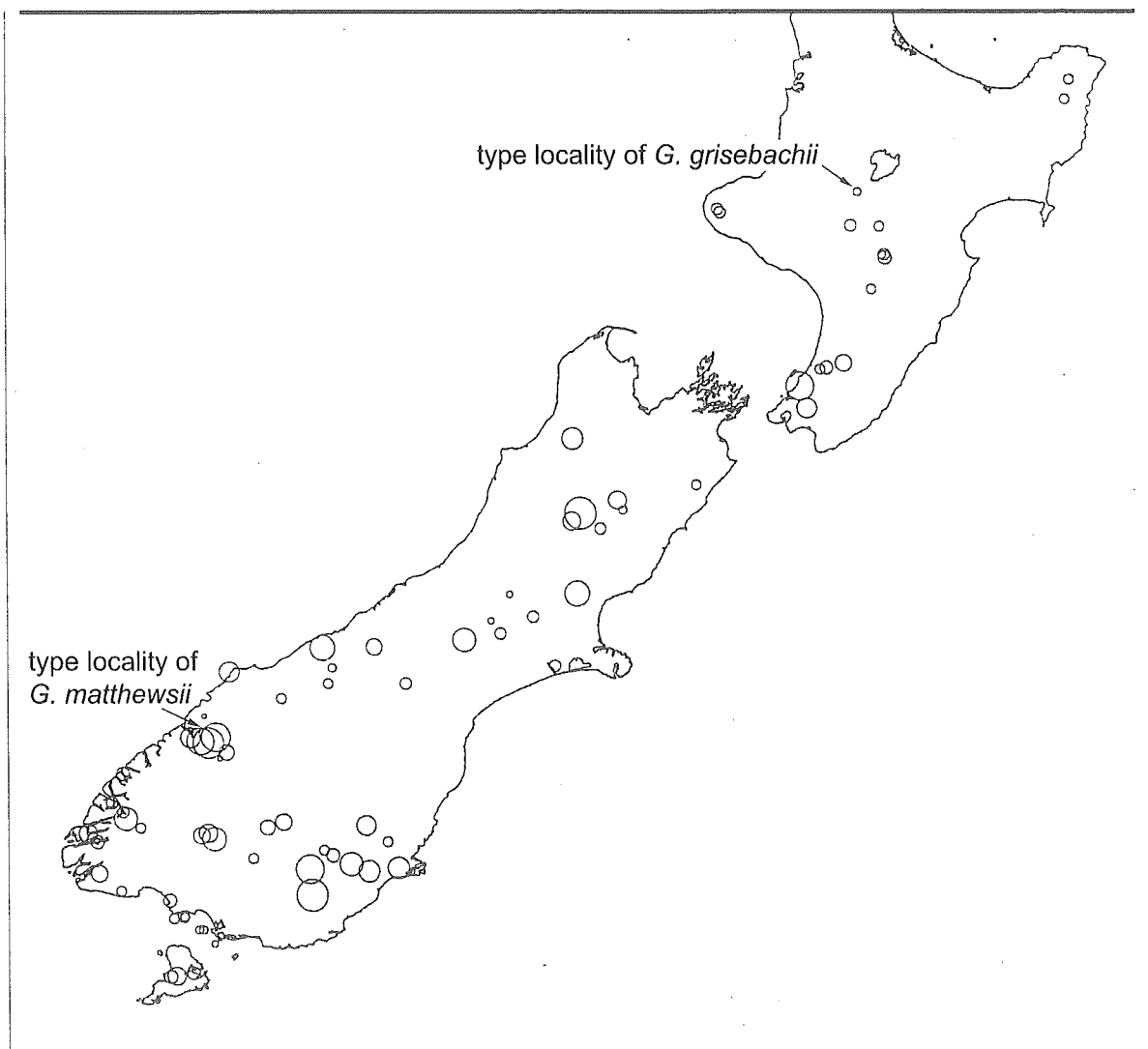


Fig. 21 Metroglyph showing variation in leaf length in *Gentianella grisebachii* – *Gentiana matthewsii* complex in New Zealand. The diameter of the circles is proportional to the length-to-width ratio of the calyx.

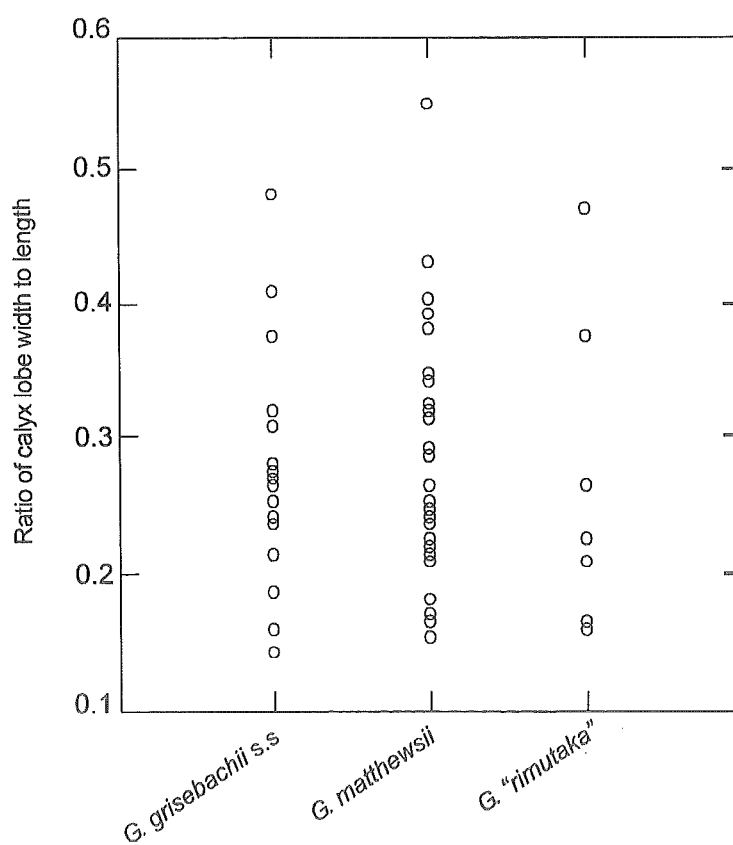


Fig. 22 Ratio of calyx width to length ratio for individual specimens of *Gentianella grisebachii* s. s., *Gentiana matthewsii*, and *G. 'rimutaka'*.

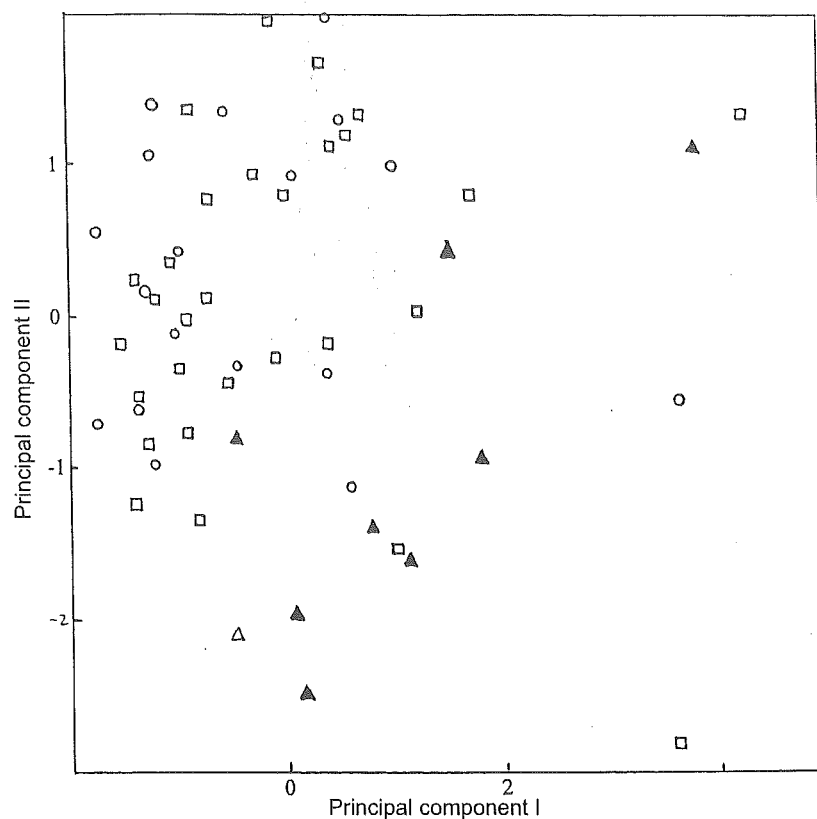


Fig. 23 Principal components analysis of the *Gentianella grisebachii* complex, components I and II. ○ = *G. grisebachii*, ▲ = *G. "rimutaka"*, □ = *G. matthewsii*.

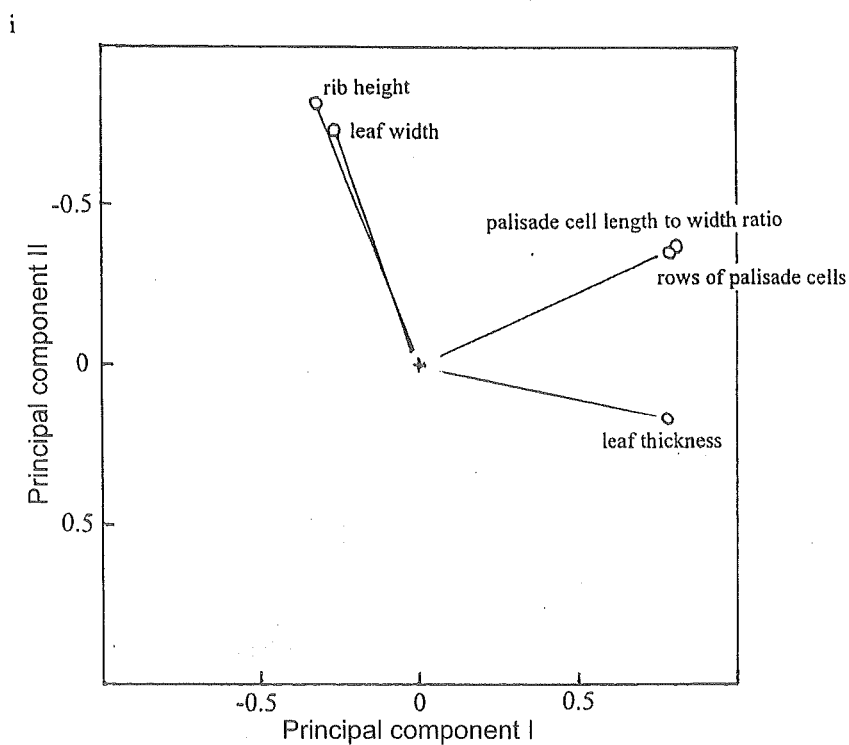


Fig. 24 Component scores for characters used in the *Gentianella grisebachii* complex PCA, components I and II.

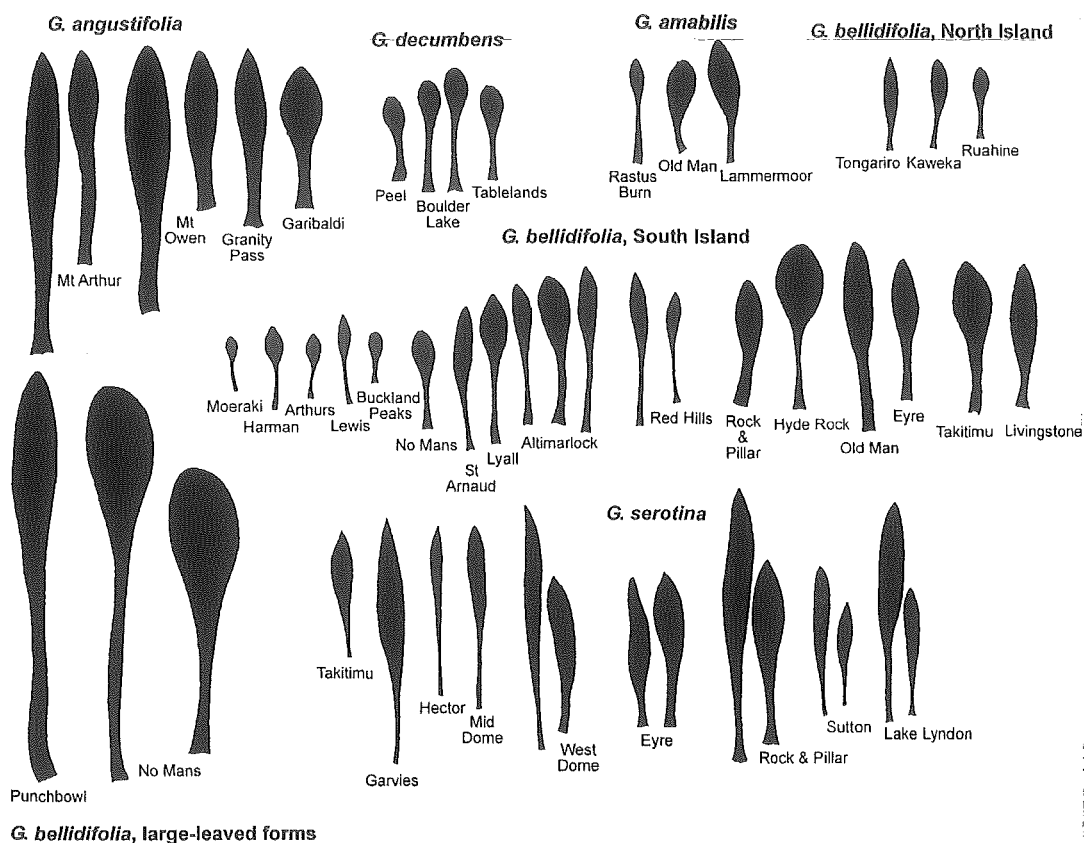


Fig. 25 Leaf silhouettes of species of the *Gentianella bellidifolia* group.

G. angustifolia: Mt Arthur: *D. Glenny* 7440, CHR 560068; Mt Owen: *D. Glenny* 7367b, CHR 559994; Granity Pass: *D. Glenny* 7365, CHR 559991; Garibaldi Ridge: *D. Glenny* 7418, CHR 560049. *G. decumbens*: Peel Range: *D. Glenny* 7437, CHR 560059; Boulder Lake: *D. Glenny* 8103b, CHR 565236; Mt Arthur Tablelands: *A. P. Druce*, CHR 277645. *G. amabilis*: Rastus Burn: *D. Glenny* 6862, CHR 559424; Old Man Range: *D. Glenny* 6887, CHR 559448; Lammermoor Range: *C. Jensen*, CHR 526407. *G. bellidifolia*, North Island: Tongariro: *I. Breitwieser* 2081, CHR 526297; Kaweka Range: *M. J. Bayly* 880, CHR 516237; Ruahine Range: *S. Wagstaff* 97-130, CHR 526418. *G. bellidifolia*, large-leaved forms: Punchbowl Creek: *D. Glenny* 8604, CHR 542509; No Mans Creek: *D. Glenny* 6899, CHR 530572; *G. bellidifolia*, South Island: Moeraki: *D. Glenny* 7383, CHR 560013; Harman Pass: *D. Glenny* 6931, CHR 530600; Arthur's Pass: *D. Glenny* 6428, CHR 509955; Lewis Pass: *M. Newfield*, unvouchered; Buckland Peaks: *D. Glenny* 6450, CHR 509977; No Mans Creek: *D. Glenny* 6898, CHR 530571; St Arnaud Range: *G. Jane*, unvouchered; Rahu Stream: *P. Wardle*, CHR 565237; Altmarlock: *K. Hogan* 1, CHR 526402; Red Hills: *D. Glenny* 6432, CHR 509959; Waikaia Bush Road: *P. N. Johnson* 1370, CHR 511798; Rock and Pillar Range: *P. D. Scott*, OTA 036452; Hyde Rock: *D. R. Given* 14216, CHR 420574; Old Man Range: *P. N. Johnson* 1373, CHR 511801; Eyre Mountains: *R. McKenzie*, CHR 518954; Takitimu Mountains: *B. Rance*, CHR 526414; Livingstone Mountains: *P. N. Johnson* 1398, CHR 526298. *G. serotina*: Takitimu Mtns: *B. Rance*, unvouchered; Garvies: *D. Glenny* 6381, CHR 509907; Hector Mtns: *K. J. M. Dickinson* & *A. F. Mark*, OTA 43965; Mid Dome: *K. J. M. Dickinson* & *A. F. Mark*, OTA 43965; West Dome: *P. N. Johnson* 1364, CHR 511792; Eyre Mtns: *B. D. Rance*, Helen Peaks, Eyre Mountains, CHR 516252; Rock and Pillar Range: *N. Simpson*, CHR 472159; Sutton: *H. Aitchison*, OTA 2643; Lake Lyndon: *D. Glenny* 6429, CHR 509956.

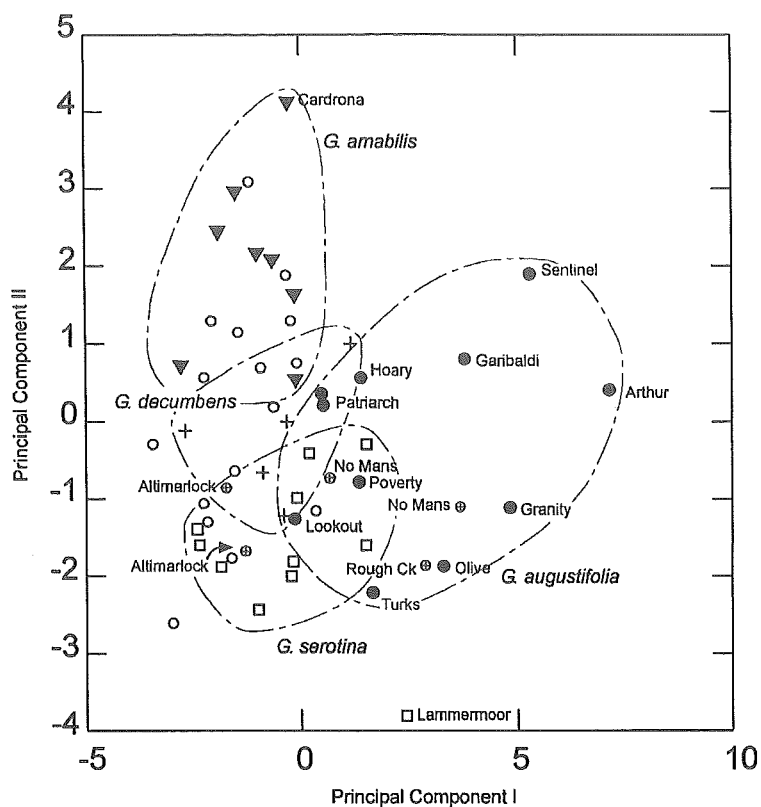


Fig. 26 Principal components analysis of *Gentianella bellidifolia* group, components I and II. ▼ = *G. amabilis*, □ = *G. serotina*, + = *Gentiana* "decumbent", ● = *G. "long narrow leaves"*, ⊗ = large-leaved forms of *Gentianella bellidifolia* from non-marble sites, ○ = *G. bellidifolia* s. s.

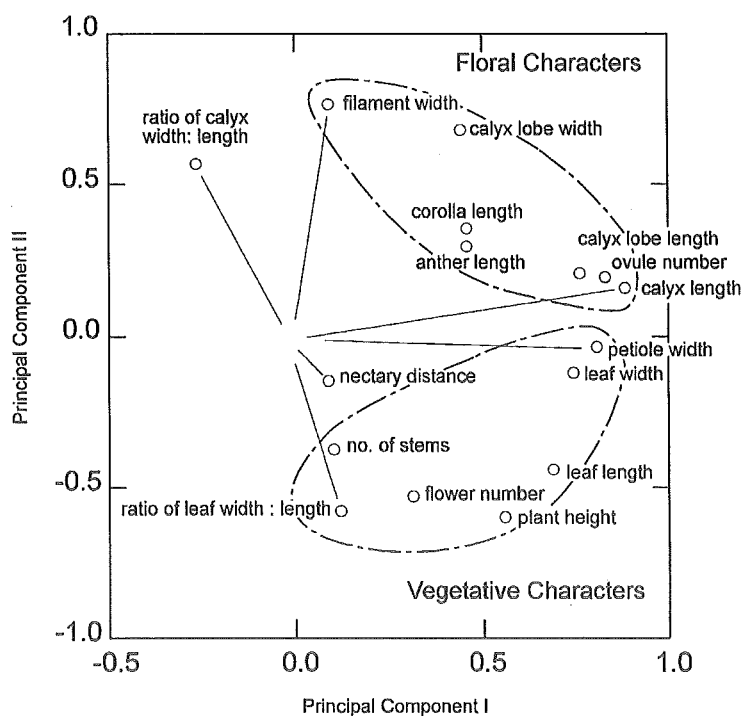


Fig. 27 Component scores for characters used in the *Gentianella bellidifolia* group PCA, components I and II.



Fig. 28 *Gentianella decumbens*. D. Glenny 7437, Peel Range, CHR 560059. Drawing by Tim Galloway.



Fig. 29 *Gentianella bellidifolia*. A. Wilton 99105B, Ruapehu, unvouchered. Drawing by Tim Galloway.

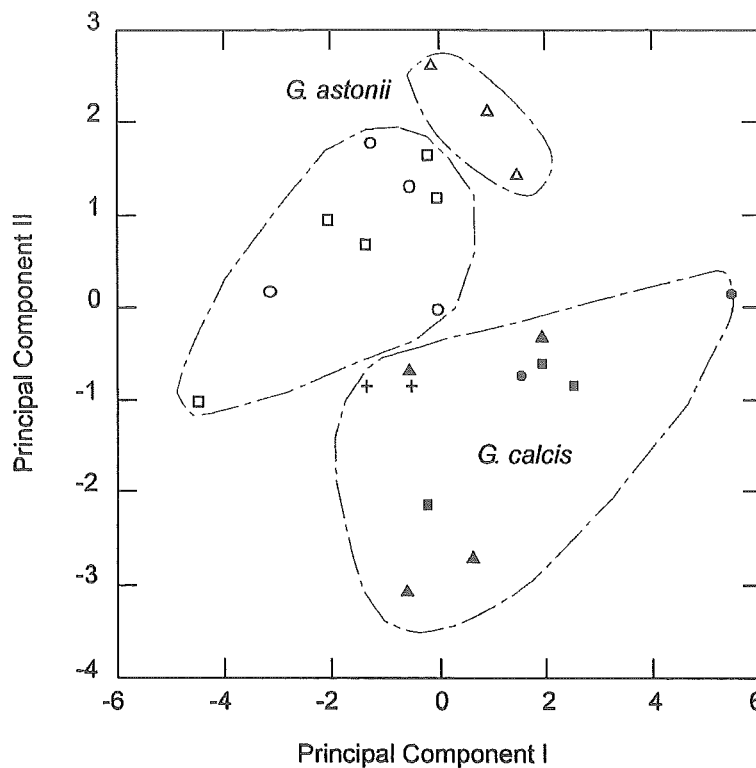


Fig. 30 Principal components analysis of *Gentianella astonii* group using 11 quantitative characters, components I and II.
 Δ = *G. astonii* s. s., \square = *Gentiana* "Chalk", \circ = *G.* "Ward", \bullet = *G.* "Awahokomo", \blacktriangle = *G.* "Brown", \blacksquare = *G.* "Pareora", $+$ = *G.* "Manahune".

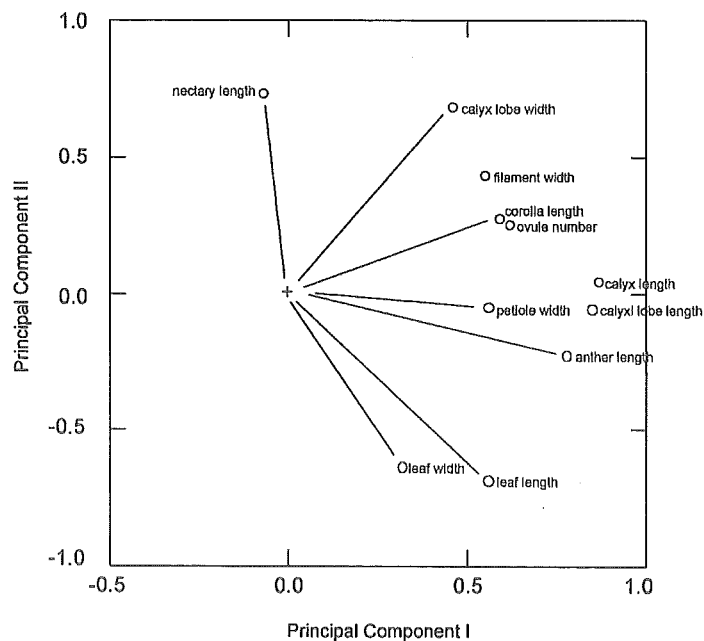


Fig. 31 Component scores for characters used in the *Gentianella astonii* group PCA using 11 quantitative characters, components I and II.

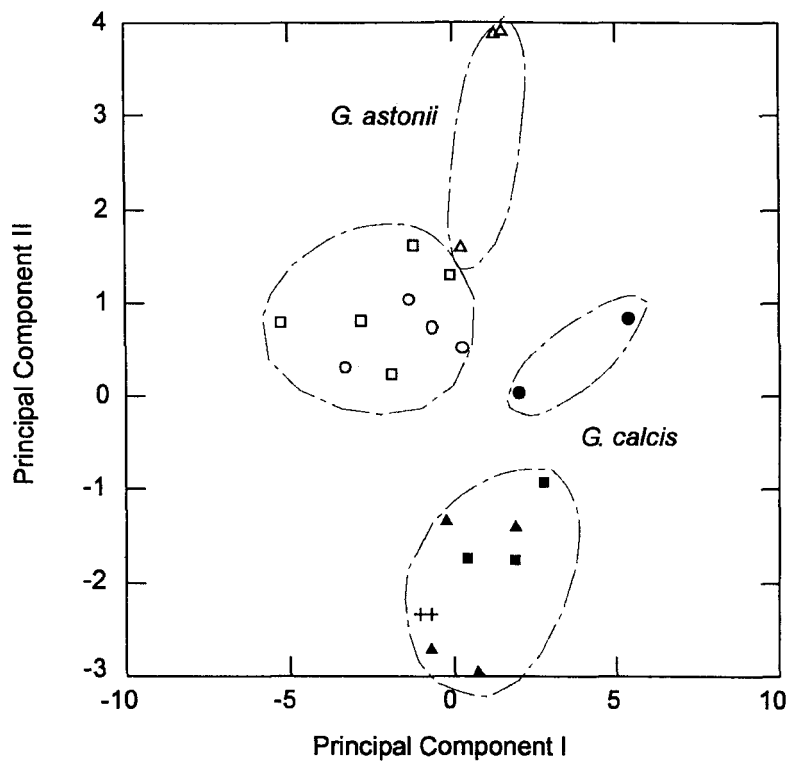


Fig. 30 Principal components analysis of *Gentianella astonii* group using 20 quantitative and qualitative characters, components I and II. Δ = *G. astonii* s. s., \square = *Gentiana* "Chalk", \circ = *G.* "Ward", \bullet = *G.* "Awahokomo", \blacktriangle = *G.* "Brown", \blacksquare = *G.* "Pareora", $+$ = *G.* "Manahune".

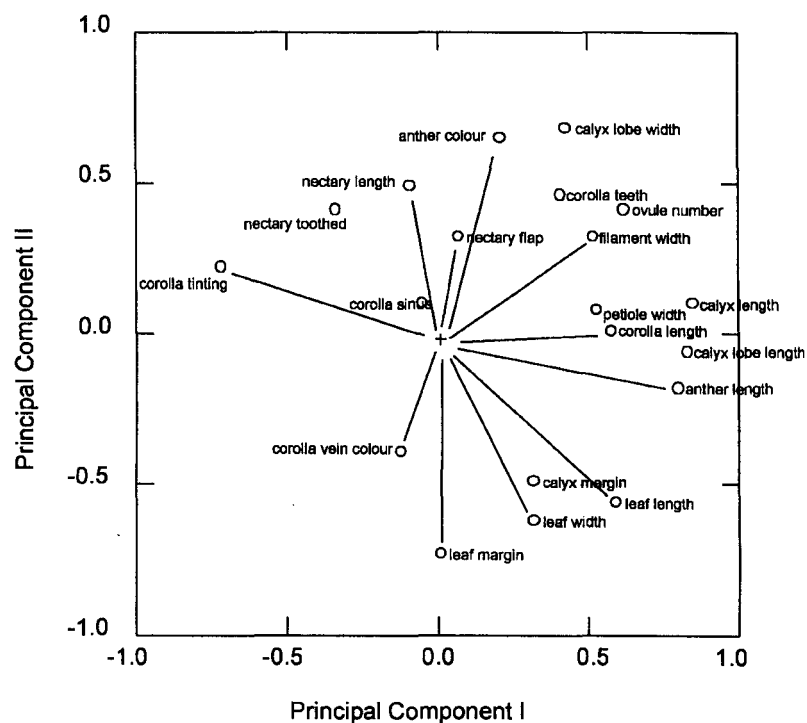


Fig. 33 Component scores for characters used in the *Gentianella astonii* group PCA using 20 characters, components I and II.



Fig. 34 *Gentianella calcis* ssp. *waipara*, Mt Brown.

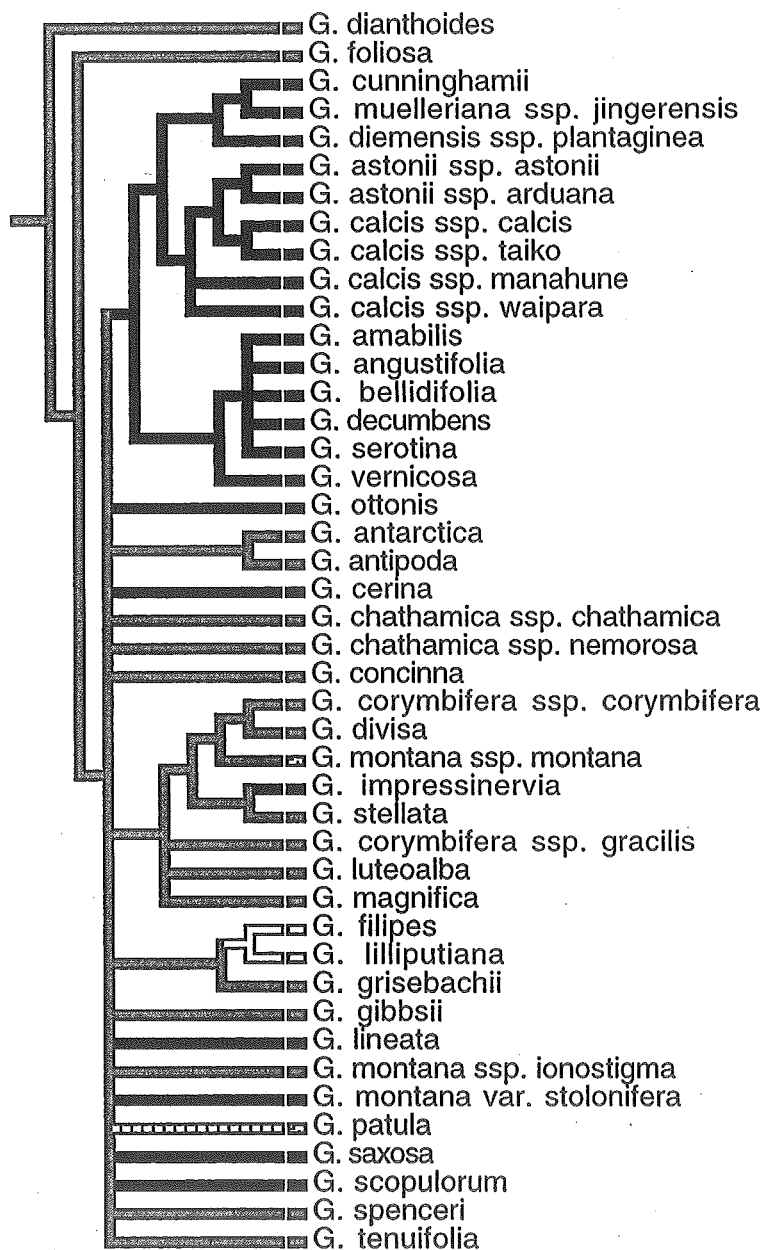


Fig. 35 Strict consensus of shortest trees from parsimony analysis using 31 characters. Produced by consenxus of 15 198 trees of 163 steps from a search of 20 000 trees.

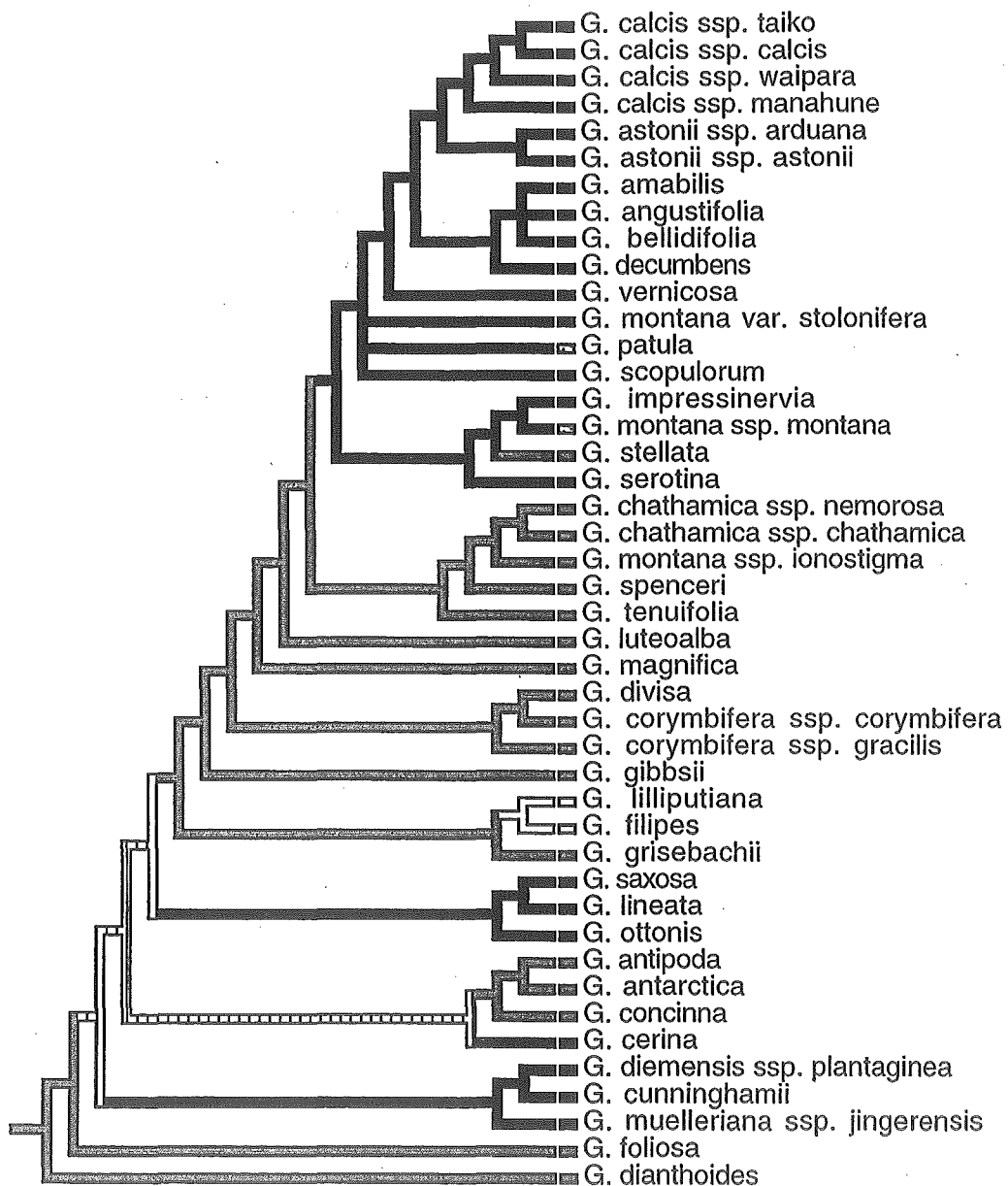


Fig. 36 Strict consensus of shortest trees from parsimony analysis using 32 characters including New Zealand distribution. Produced by consensus of 10 trees of 187 steps from a search of 20 000 trees.

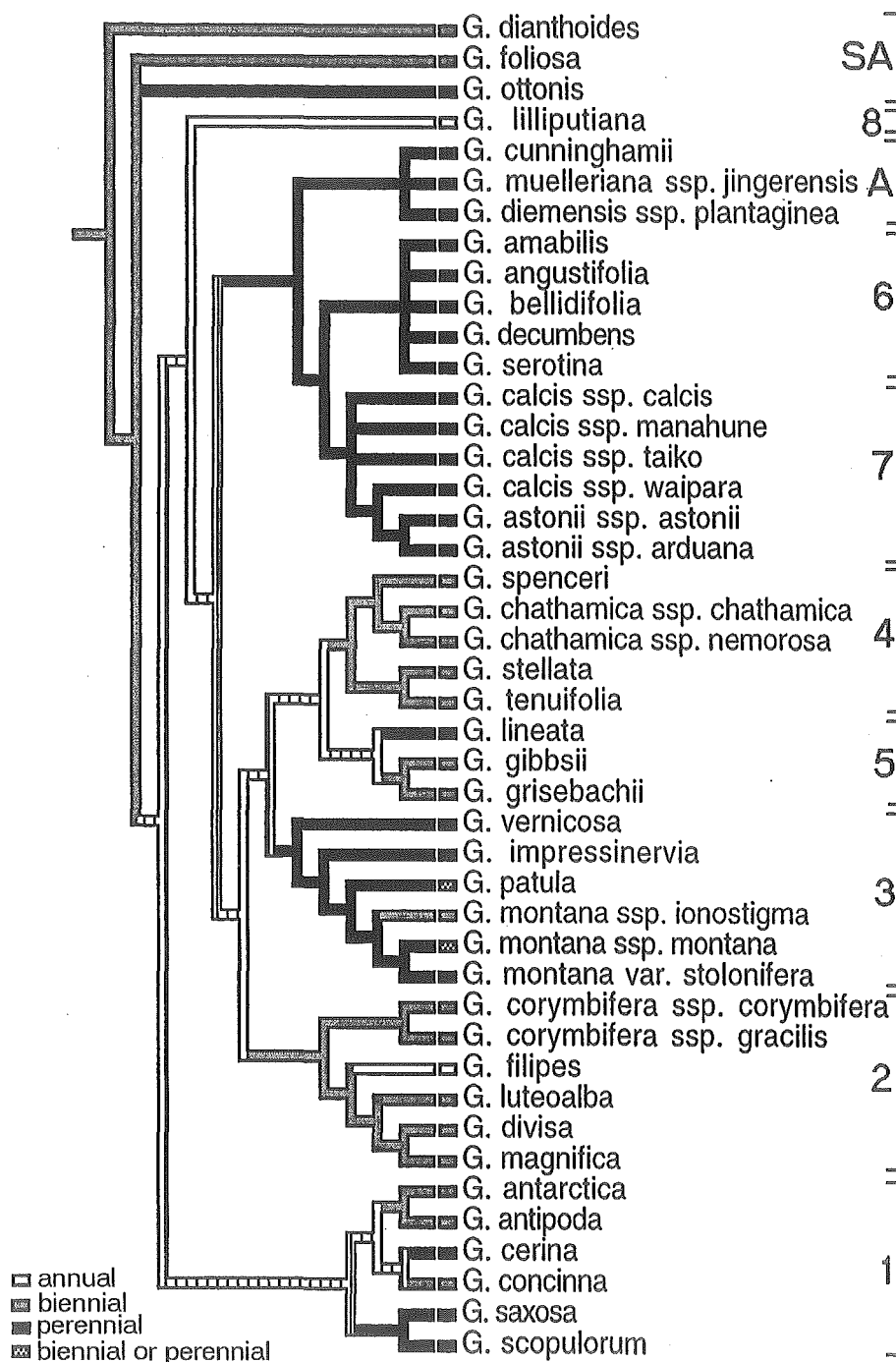


Fig. 37 Intuitive phylogeny of New Zealand *Gentianella* and including some Australian and South American species. Life-cycle has been mapped onto the tree. Relationships are conveyed only by the branching structure, not branch lengths. SA = South American species, A = Australian species, 1 = *G. saxosa* group, 2 = *G. divisa* group, 3 = *G. montana* group, 4 = *G. spenceri* group, 5 = *G. grisebachii* group, 6 = *G. bellidifolia* group, 7 = *G. astonii* group, 8 = *G. lilliputiana* group.

	10	20	30	40	50	60
<i>G. impressinervia</i>	123456789	123456789	123456789	123456789	123456789	1234567
<i>G. astonii</i> ssp. <i>astonii</i>	GTGCCAAATCTCTTCAGGGACGGACCTCATGGCGCCGCAATGCGACCCCGATAACCCACCGTGTCT					
<i>G. bellidifolia</i> 1	..A.....G...	RT.....	C.....		
<i>G. bellidifolia</i> 2	..A.....G.....	T.....	G.....	G.....	C.....	
<i>G. montana</i> var. <i>stolonifera</i>	..A.....	G.....	A.....			
<i>G. chathamica</i> ssp. <i>chathamica</i>	..A.....G.....		G.....	??????????		
<i>G. grisebachii</i>	..A.....G.....	T.....	G.....	A.....	C.....	G.....K
<i>G. corymbifera</i> 1	..A.....G.....	A.????????	????????	????????	????????	????????
<i>G. corymbifera</i> 2	..A.....G.....	G.....	Y.....	RR.....		
<i>G. spenceri</i>	..A.....K.....	S.....	G.....			Y..Y
<i>G. serotina</i>	..A.....G.....	T.....	G.....	G.....		C
<i>G. lilliputiana</i>	..A.....G.....	C.G.....	T-AG.....	T...T...	A.G..AT.....	
<i>G. lineata</i>	..A.....G.....	T.....	G.....	G.....		C
<i>G. saxosa</i>	..A.....G.....	T.....	G.....	A.....	G.....	C
<i>G. antipoda</i>	..A.....G.....	T.T.....	G.....	T.....	G.....	
<i>G. antarctica</i>	????..G.....	T.T.....	G.....	????????	????????	??????
<i>G. cerina</i>	..A.....G.....	T.....	G.....	G.....		
<i>G. magellanica</i> (SA)	..A.....G.....	A..T.....	G...?	T.T....	G.....	T.
<i>G. magellanica</i> (SA)	..A.....G.....	A..T.....	G...?	T.T....	G.....	T.
<i>G. narcissoides</i> (SA)	..AT....G....	Y..A.....	G.....	G.....		
<i>G. sp.</i> (SA)	???..G.....	T..G..A.....	????????	????????	????????	??????
<i>G. myriantha</i> (SA)	..AT....G.....	G...T.....		GW...?	??????	
<i>G. diemensis</i> s.s. (A)	..A.....G.....	G.T.....	T...A..T...	G....A..T-		
<i>G. polysperes</i> (A)	..A.....G.....	?.?.....	A..T...G....	A.....G...		
<i>G. pleurogynoides</i> (A)	..A.....G.....	G.K.....	T...A..T...G..	G.A.....G...		
<i>G. muelleriana alpestris</i> (A)	..A.....G.....	G.....	A..T...G..G.A.			
<i>G. biebersteinii</i> (E)	..AA.TG.GG..A.C..A.A..A...	G.....	C..A.....G....	T.A...C..		
<i>G. caucasea</i> (E)	..AA.TG.GGT...C..A.A..A...	G.....	C..A.....G....	T.A...C..		
<i>G. campestris</i> (E)	..T.A.T..GG.....A.A..A..CG...	C....C..G.....	TG.....A...C..			
<i>G. umbellata</i> (E)	..A...TGG.G.C.A.A.A..G....	C.TT.....	T...G....ACGC...			

Ambiguity codes: G/T = K; C/T = Y; A/G = R; C/G = S; A/T = W.
Geographical codes: SA = South America; A = Australia; E = Europe.

Fig. 38 Variable sites in ITS1, 5.8S, and ITS2 rDNA region in *Gentianella*.

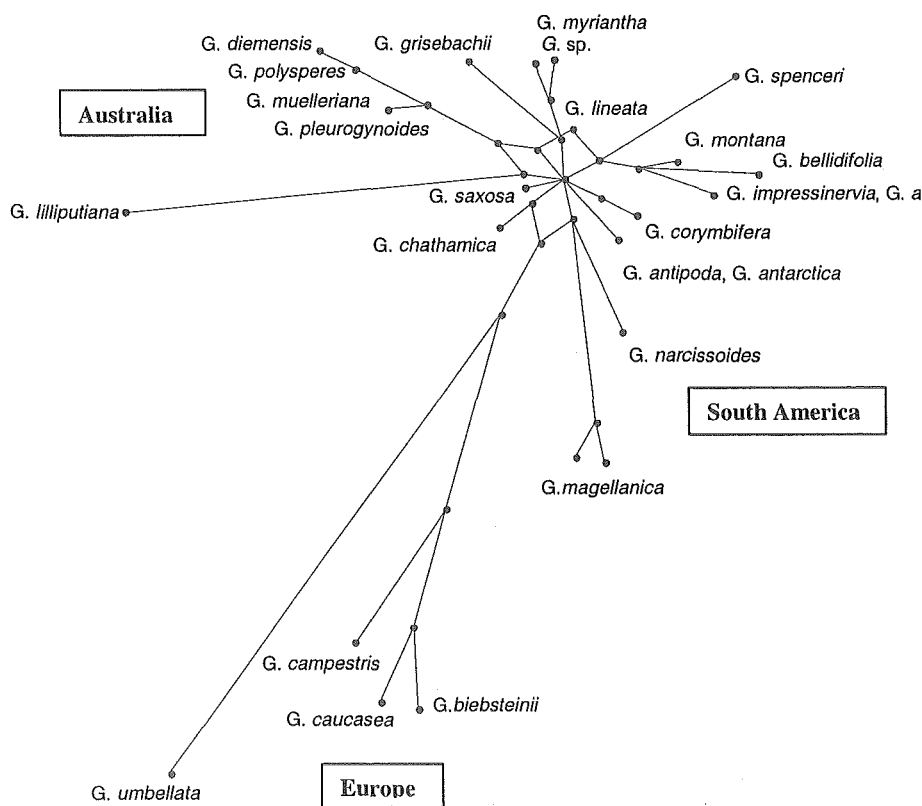


Fig. 39. Median network derived from ITS DNA sequences of 24 species. At the centre of the radiation in the upper part of the network are three species that are not labelled: *Gentianella serotina*, *G. bellidifolia*, and *G. cerina*. Sequences of species that are not Australian, South American, or European are from New Zealand.

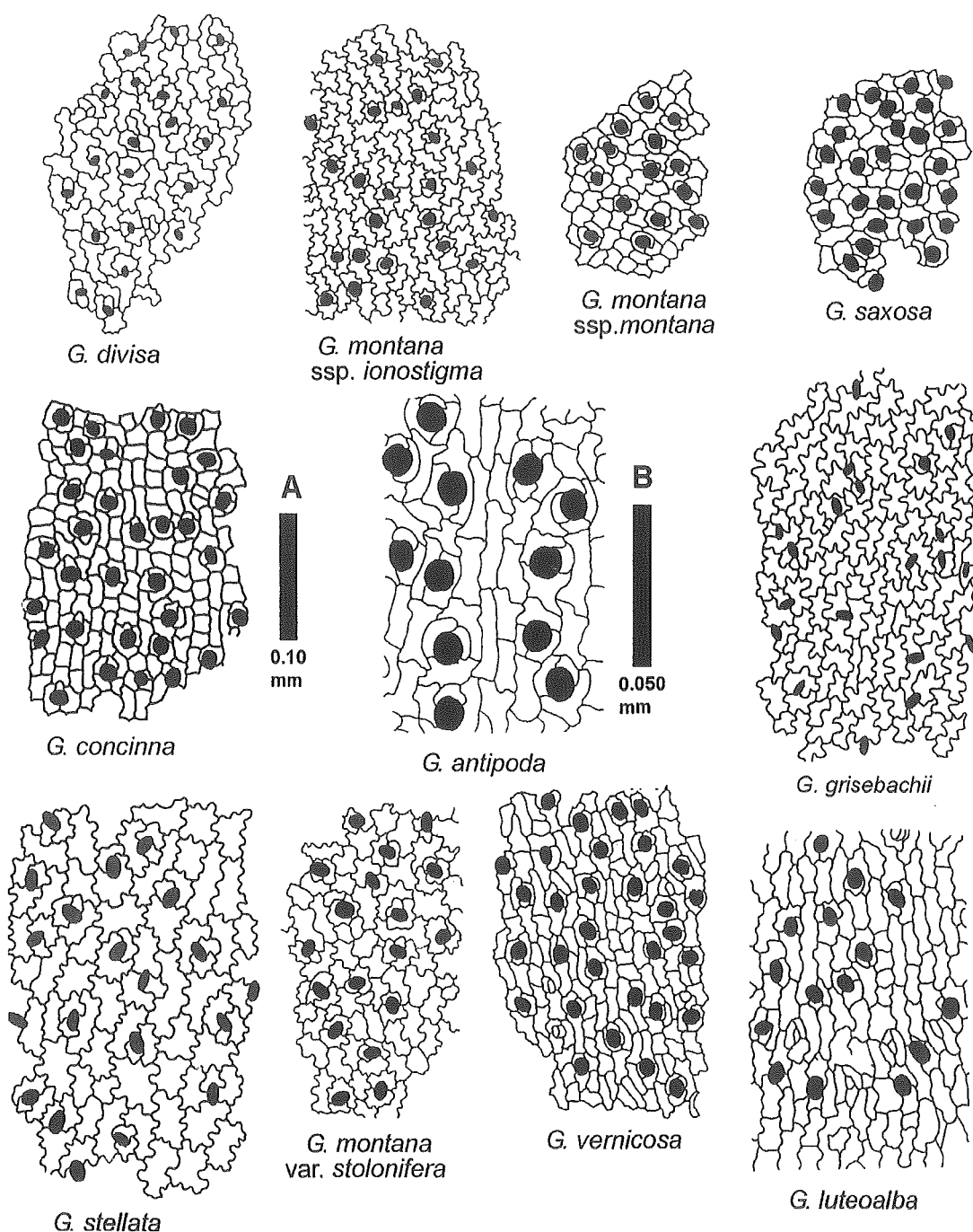


Fig. 40 Leaf epidermal cell shapes in some New Zealand *Gentianella* species. S is the shape factor. The black areas show the position of the guard cells, and were filled to allow the image analyser to ignore them while calculating the shape factor of the other cells. Scale bar B applies to *G. antipoda*, scale bar A applies to all other cuticle drawings.

G. divisa, S = 0.53, *G. Spearpoint*, Shotover Saddle, CHR 526417; *G. montana* ssp. *ionostigma*, S = 0.41, *I. Breitwieser* 2062, Mt Hikurangi, CHR 526397; *G. montana* ssp. *montana*, S = 0.58, *D. Glenny* 7357, Lookout Range, CHR 559983; *G. saxosa*, S = 0.54, *D. Glenny* 6372, Big Bungaree Beach, CHR 509898; *G. concinna*, S = 0.60, *C. Meurk*, Auckland Is., CHR 526412; *G. antipoda*, S = 0.39, *E. J. Godley*, Antipodes Is., CHR 549027; *G. grisebachii*, S = 0.38, *P. N. Johnson* 1407, Livingstone Mountains, CHR 515002; *G. stellata*, S = 0.40, *G. Jane*, Croisilles Harbour, CHR 516246; *G. montana* var. *stolonifera*, S = 0.39, *P. Suisted*, Croesus Knob, CHR 516249; *G. vernicosa*, S = 0.52, *D. Glenny* 7367a, Sentinel Hill, CHR 559993; *G. luteoalba*, S = 0.51, *D. Glenny* 7415, Lookout Range, CHR 559987.

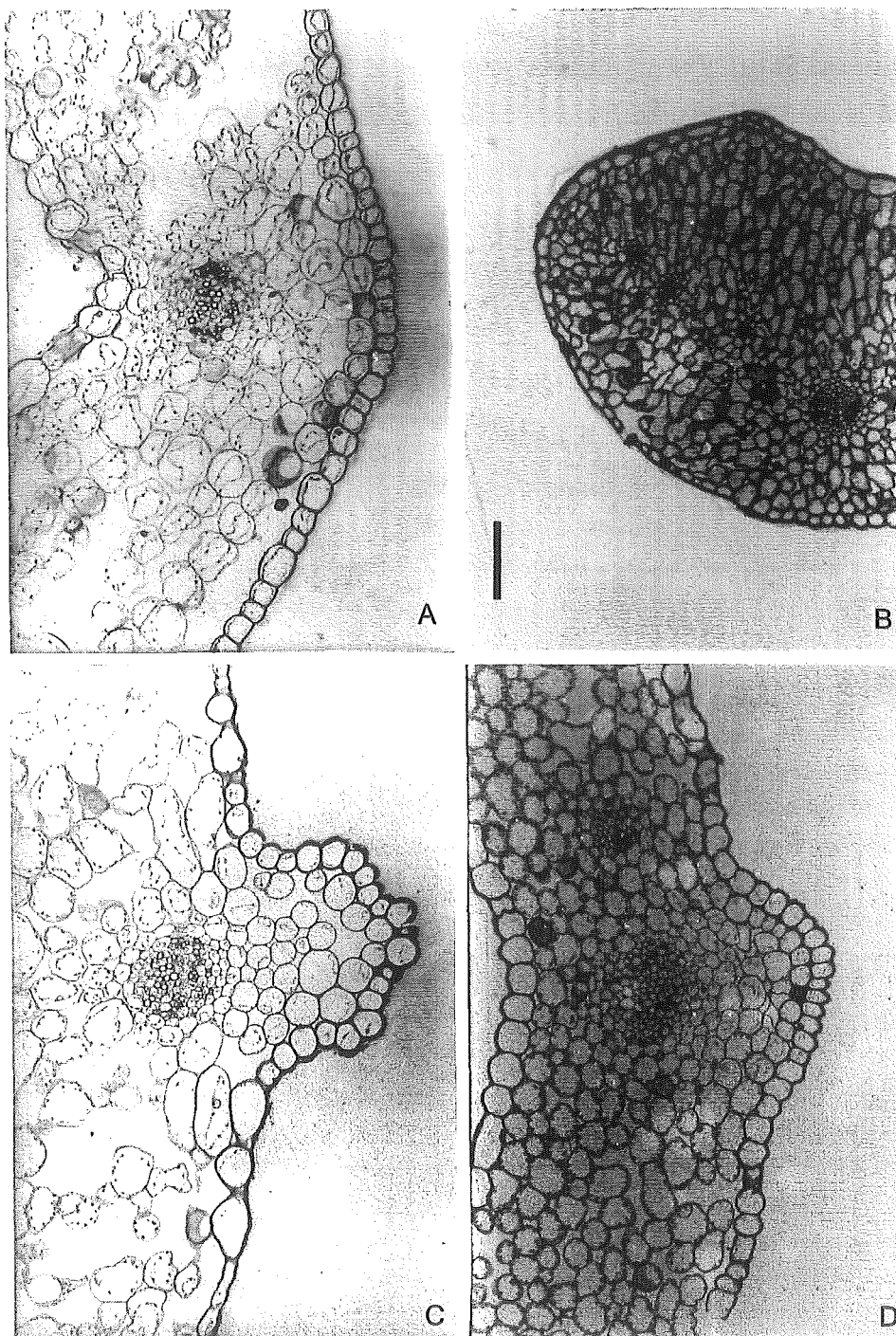


Fig. 41 Leaf transverse sections of some New Zealand *Gentianella* species. Scale bar in B is 0.1 mm and applies to all four photographs.

A. *G. concinna*, showing epidermal cells of uniform size, the lack of a projecting midrib, and large internal air gaps. C. Meurk, Enderby Is., CHR 526412.

B. *G. astonii* s. s. showing a thick, narrow leaf with well-developed palisade cells and lack of a projecting midrib. D. Glenny 6416, Isolated Creek, CHR 509942.

C. *G. chathamica* s. s. showing a projecting midrib and epidermal cells of unequal depth and diameter. P. J. de Lange CH21, Chatham Is., CHR 510011.

D. *G. divisa* showing an absence of elongated palisade cells. K. Wardle, Ferguson Creek, CHR 526440.

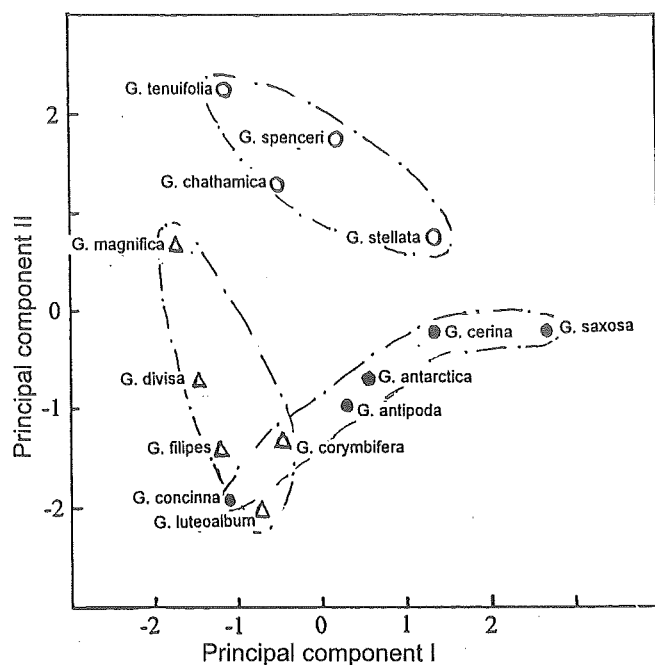


Fig. 42 Principal components analysis of New Zealand *Gentianella* taxa using four leaf anatomy characters, *G. spenceri*, *G. divisa*, and *G. saxosa* groups.

○ = *G. spenceri* group, ● = *G. saxosa* group, △ = *G. divisa* group.

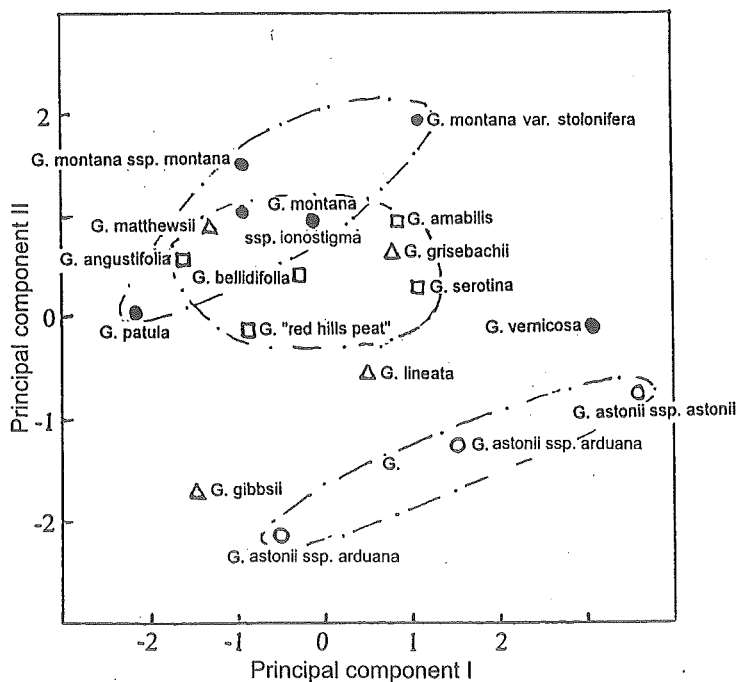


Fig. 43 Principal components analysis of New Zealand *Gentianella* taxa using four leaf anatomy characters, *G. montana*, *G. bellidifolia*, *G. grisebachii*, and *G. astonii* groups.

○ = *G. astonii* group, ● = *G. montana* group, △ = *G. grisebachii* group, □ = *G. bellidifolia* group.

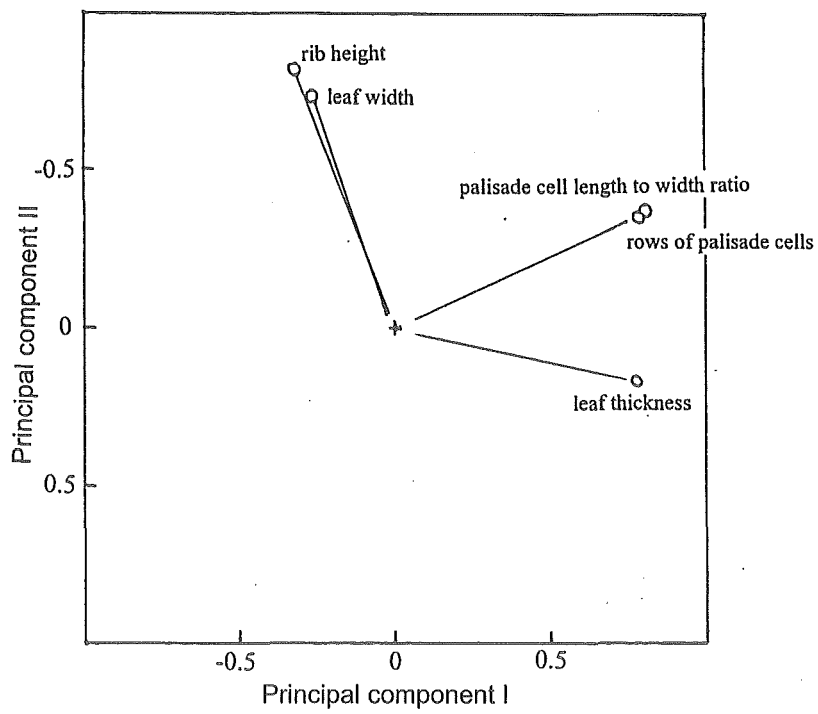


Fig. 44 Component scores for principal components I and II in leaf anatomy PCA.

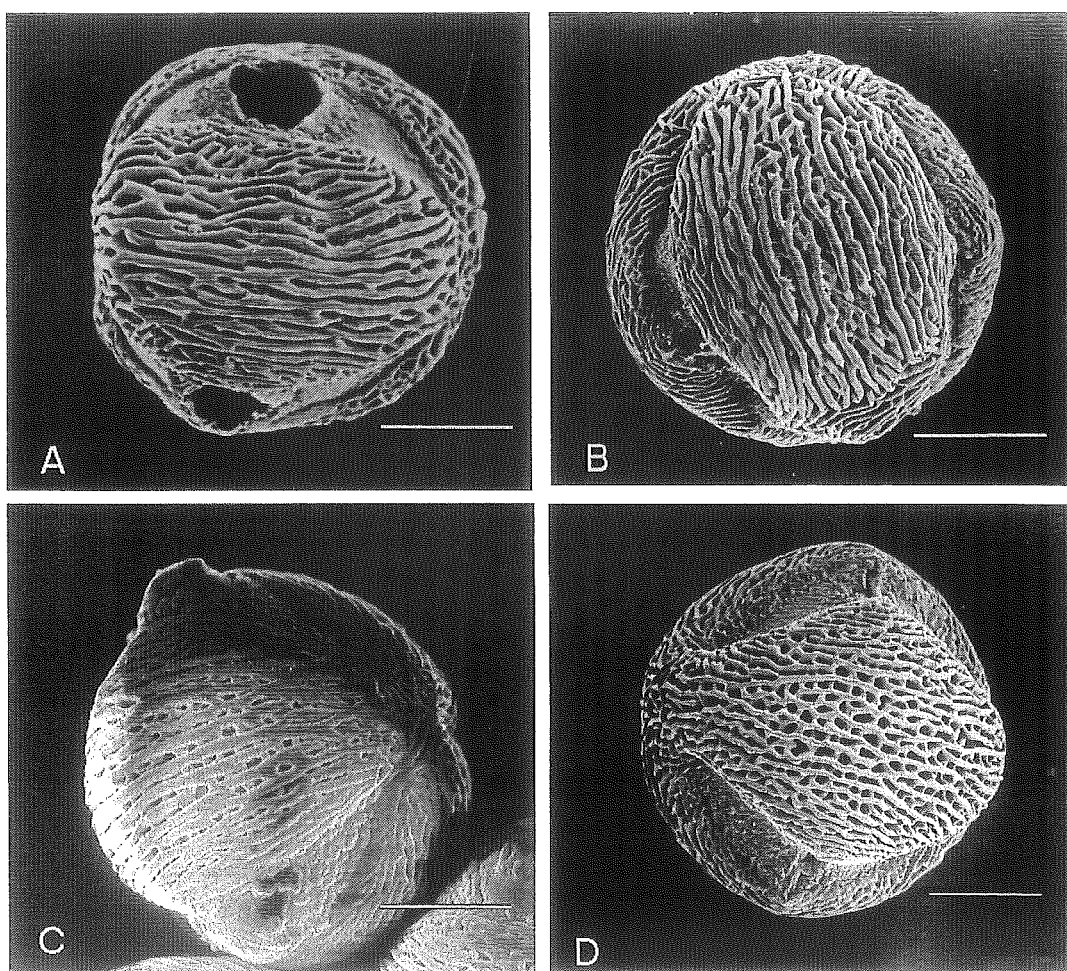


Fig. 45 Pollen grains of New Zealand, South American, and Australian *Gentianella* species. A. *G. antarctica*, D. Given 9364, Campbell Is., CHR 284293; B. *G. montana*, B. Sneddon, Mt Arthur, WELTU 15673; C. *G. impressinervia*, A. P. Druce, Glasgow Range, CHR 394530; D. *G. serotina*, C. J. Webb 76117, Lake Lyndon, CHR 283763. Scale bars are all 10 μm . Photos A and D: Siwert Nilsson, Palynological Laboratory, Swedish Museum of Natural History, SE-104 05 Stockholm, Sweden.

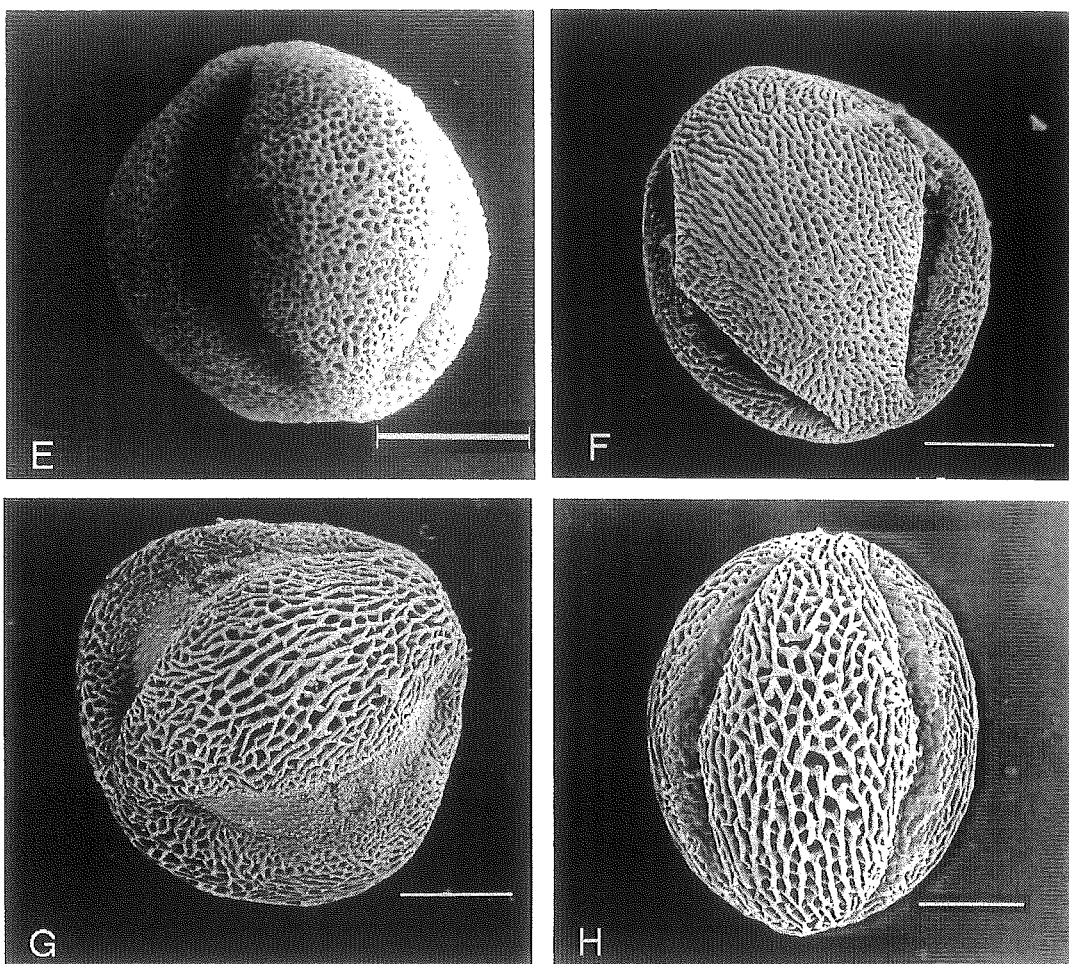


Fig. 45 continued Pollen grains of New Zealand, South American, and Australian *Gentianella* species.

E. *G. lilliputiana*, D. Bruce, Lauder Creek, CHR 418480; F. *G. lineata*, A. Mark, Ajax Bog, CHR 364169; G. *G. foliosa*, S. Laegaard 53880, Vulcan Atacazo, QCA; H. *G. diemensis*, A. T. Dobson 77124, Newdegate Pass, CHR 314353. Scale bars are all 10 μm . Photos F, G, and H: Siwert Nilsson, Palynological Laboratory, Swedish Museum of Natural History, SE-104 05 Stockholm, Sweden.

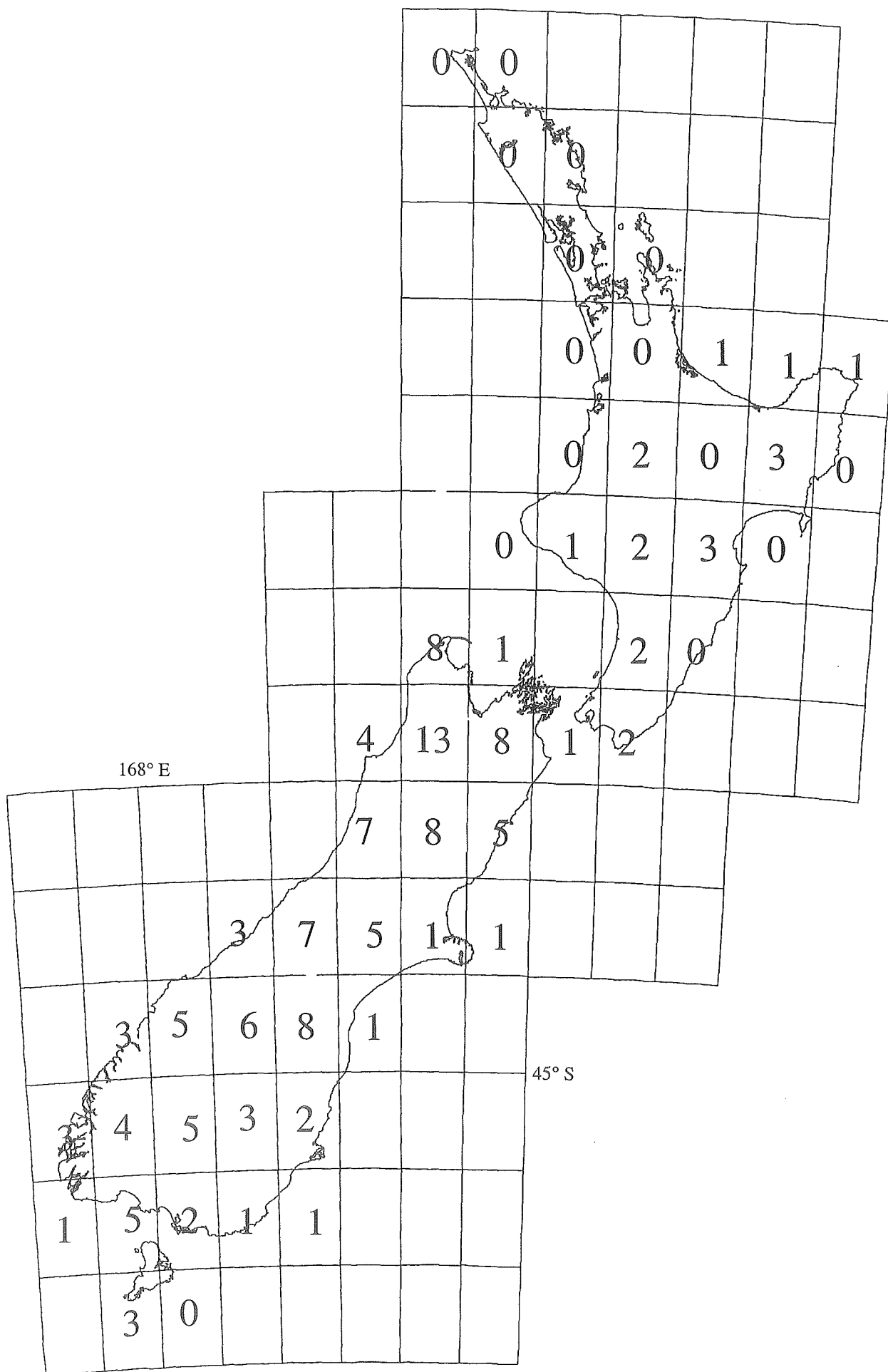


Fig. 46 Density of *Gentianella* taxa in New Zealand. Number of taxa are given in each one degree square.

DISCUSSION AND CONCLUSIONS

In the Introduction, a number of issues that arise in the course of revision of a genus were raised. The issues of the genus concept, species concept, infraspecific rank were discussed. Methods of quantitative analysis useful to taxonomic work were discussed. The use of microscopic and submicroscopic characters was discussed. The contributions of distribution, habitat ecology, and floral biology were also discussed. In this section, issues that arose from reviewing the literature on these issues are related to the revision of New Zealand *Gentianella*. I compare this revision with the other two country revisions of *Gentianella* done for Australia (Adams, 1995) and North America (Gillett 1957).

The status of this revision

In this work, I have attempted to provide a revised classification for all New Zealand *Gentianella* species, a full synonymy that accounts for all types, comprehensive descriptions of every species and subspecies, a natural key and artificial keys, and distributional information, notes on habitat, and flowering time.

In addition to these basic requirements for a revision, I have stated how characters were used, analysed quantitative characters, shown how taxonomic decisions were made, and indicated where difficulties were. Areas of uncertainty have been highlighted. I have attempted to interpret the evolution of the group and have expressed this in the construction of informal groups. I am unable to offer a well supported phylogeny. I have interpreted the biogeography of the group, dealing with issues of the group's origin, the timing of its radiation, and the trends in the group's characters related to the ecological niches of the species.

These additions to what is required by a revision are often found in a monograph, but this work falls short of being a comprehensive monograph in three respects: the New Zealand gentians are only part of the genus *Gentianella*, and if I am correct in supposing that the Australian species have their origin from a New Zealand species, the New Zealand species are a paraphyletic group. Secondly, breeding experiments were not done for this revision, so that information on hybridisation and an assessment of its importance in speciation in the group is lacking. In other revision of *Gentianella*, neither Adams (1995) nor Gillett (1957) addressed hybridisation as an issue in their regions, although Gillett considered in individual cases that hybridisation occurred in the North American gentians. Because of this lack of genetic evidence, I

have had to use what Davis & Heywood (1963) called the morphological-geographical species concept. The limitations of this are most apparent in my uncertainty over the taxonomic rank of some forms in the *G. bellidifolia* group. Thirdly, a complete and robust phylogeny of New Zealand *Gentianella* is not provided.

The genus concept

On this issue there is a major conceptual gap between those of a more or less phenetic point of view who see groups above species level in terms of similarities and discontinuities, and those of a cladistic point of view for whom monophyly is the basic criterion.

In my view, monophyly is a much better criterion to use for defining groups above species level than a gap or discontinuity to the nearest taxon used by authors such as Stuessy (1990) or Davis & Heywood (1963) for the reason that monophyly is an unambiguous quality of a group, while gaps and discontinuities are not. It also appears now to be a practical criterion in most groups of plants that undergo revision. However, a problem that may become more apparent with this criterion in the near future is that the clades we call genera, like species, may not bifurcate from each other as cleanly as our tree diagrams have depicted. The lack of resolution provided by DNA sequences at the base of radiations of some New Zealand groups of genera may be a widespread problem, making monophyly an impractical criterion for genera in some cases.

A second issue is whether the clades we call genera are natural or biological groupings. Because the rank of genus is a compulsory one, genera must be made regardless of whether such groupings exist. Bentham (cited in Stevens 1997) appeared to think that genera were units of convenience. The taxonomists who expressed a view to Anderson (1940) were clearly of the opinion that these groupings were more natural than species. Present day opinion seems to have returned to the view of Bentham. My own opinion is that in many cases these natural groups do exist. That is, there are monophyletic groups that are very distinct from the species that are closely related. Expressed in a different way, there is significant clumping. This probably most often results when an adaptive radiation occurs after a dispersal event to a new and largely unoccupied environment, and all species share some distinctive functional features. In this sense, a genus can be a biological entity. Biologists have recognised this and attempted to include this in their criteria for genus recognition. A problem with such radiations is that they often arise from a species that lies within another clade identified as a genus. If the newly radiated group is recognised as a genus, it makes the group it is

nested within paraphyletic.

Because genus rank is compulsory, many genera have been made that do not exhibit naturalness in the sense of phenetic distinctness (even if they are monophyletic). In some groups of plants, homoplasy may be so rife that no monophyletic groups can be selected that show universally shared character states. DNA sequence-based phylogenies sometimes show that even when the basic requirement of monophyly is observed, there may be no single obvious arrangement into genera based on defining morphological character states. The Phylocode has in its favour that these more artificial genera would not need to be recognised.

These considerations show why it seems that genera both reflect both biological groupings and can appear to be merely convenient groupings, and that the remodelling of existing genera involves a tension between the desire to reflect descent and the need to produce a useful classification that conforms to the existing Code of Botanical Nomenclature.

Various guidelines on the recognition of genera can be found, and some of these are quoted in the introduction (Judd et al. 1999; Stuessy 1994 ex McVaugh 1944; Davis & Heywood 1963; Winston 1999). These authors differ in their phenetic or cladistic perspective but their guidelines point in the same direction but disagree in detail or are couched in vague terms. Many of their guidelines are superfluous if monophyly is made a necessary condition of a genus. What has to be specified beyond the monophyly condition comes down to three criteria: (1) A 'defining character' criterion. Some authors consider that a number of shared characters is required, while others consider that a minimum of one significant character is sufficient. Some authors consider that the defining character should be universally present, while others consider that a few exceptions should not prevent it being used. For other authors, a 'family resemblance' is sufficient with no single defining character. (2) A size criterion: e.g., groups of c. 10–100 species (Bentham). There is, in practice, no agreement on this, since monotypic genera are common. But the small or large size of genera is often given as a reason for segregating or combining genera, and it is clearly a factor that is important to many taxonomists.

(3) That particular plant parts should define all the genera within a family (e.g., all the genera of a family are defined by fruit morphology as in the Juglandaceae). There seems to be such a rule in operation, although I did not find it mentioned in any of the taxonomic handbooks I examined.

An important question to ask in this is: how much does it matter? To the extent

that Bentham is correct that a classification is a matter of convenience, and an aid to memory, the rules above are useful ones. A defining character, if one is available, helps as an aid to memory, as does a genus of intermediate size.

If the arrangement of species into genera mattered a great deal, it can be hypothesised that more exact rules for recognition of genera would have been devised. The vagueness of the rules and the often cited "a genus is what a competent taxonomist considers it to be" indicate that it does not matter very much, and that in practice, we are content to use the genus rank largely as a labelling system. This function is not incompatible with insisting that genera be monophyletic, and it seems worthwhile to insist on this basic requirement. It is also not incompatible with recognising biologically natural genera of the type discussed above. But a lack of exactness in the criteria for genus recognition means that in many cases there is no objective way of deciding between some competing classifications and the literature will contain arguments over distinctness versus size that are not rationally solvable. The method of resolving these at present seems to be one of consensus by the community of users of the classifications and may depend on extrinsic factors such as the reputation of the author(s) of a classification.

A further point on this matter concerns monotypic genera. One reason for opposing monotypic genera is that sometimes they make other genus paraphyletic. A quite different reason is that they fail to meet the size criterion mentioned above. However, a classification that includes a monotype can be the automatic outcome if the monotype is positioned at the base of a larger clade that is very distinctive (Garnock-Jones, 2002) and there appears to be no possible objection to this under the present rules of nomenclature. However, under a rankless system, these monotypes need not be named as clades above species level, but could be. In the Phylocode of Cantino & de Queiroz (2001) they cannot be, unless they are part of a clade that includes fossil taxa (Cantino & de Queiroz, pers. comm. 2002).

In *Gentianella*, the segregation into a genus of the short-tubed efimbriate species could be justified if monophyly could be proved. There is just one morphological character that defines the group, the short corolla tube, and exceptions to this character are ones that can be explained by reversion. They weaken the case for its recognition not because they question the monophyly of the group, but because they question its distinctiveness. The relative length of corolla tube and corolla lobes is essentially a quantitative character, although it may be a functional one relating to pollinators, and some taxonomists would probably make such a split while others would not. Adams

(1995) thought that uniformity with the splitting of *Gentianopsis*, *Crossopetalum*, and *Conostoma* was sufficient justification for making *Chionogentias*. Hagen & Kadereit (2001) felt that while they had sampled all the distinctive groups in *Gentianella*, the resolution of their sequences and a lack of agreement between genomic regions meant that there was insufficient evidence to make such a split at present. The 270 combinations needed for a segregate genus is a reason to be conservative at this stage.

The issue of paraphyly

The kinds of evidence and methods of analysis possible now have changed the situation from the time of Allan (1953) when it could be said that similarities rather than evolutionary relationships were the firmest basis for a classification. The advent during the last twenty years of computing techniques for reconstructing evolutionary relationships and DNA sequencing techniques has changed this situation, and the change is likely to continue through improvements in both these techniques. A result of this is likely to be greater confidence in the results of DNA sequencing, and similarity will no longer seem such an obvious basis for classification.

I agree with Simpson (1961) that a natural classification is one that is consistent with the classifier's views of the phylogeny of the group, and it is desirable that the rules of nomenclature facilitate this. The arguments commonly made against this are summarised below.

(1) That phylogeny is unknowable, and that all we know is similarity (Allan 1953). This view may have been tenable in the past, but to hold this view now would be overly pessimistic. Such pessimism is best countered by looking at actual examples to see the congruence that exists between trees produced from independent data sets.

(2) That the current rules of nomenclature already make a natural classification possible. If 'natural' means taxa separated by gaps, then this is true. If 'natural' means 'composed of distinctive monophyletic groups' then this is not true for the reason explained below.

(3) That classification and phylogeny should be kept separate (Brummitt 1997). A possible justification is the argument above (1), that phylogeny is unknowable. Alternatively, it must rest on a practical objection that any extensive modification of the Code of Nomenclature is to be avoided because it will create nomenclatural instability. If this is the objection, then it is at least worth attempting to devise a code of nomenclature which minimises this instability while improving the ability of the classification to reflect phylogeny. Anyone who holds this point of view at least holds

in common with the advocate of a phylogenetic code a belief that the classification should reflect evolution.

In my view it is desirable that classifications reflect evolution as expressed in phylogenies and that similarity or difference between taxa is a weaker principal than phylogeny. For that reason, I believe a code of nomenclature should make it possible to reflect evolutionary relationships. For taxonomists to turn their back on this objective now seems to me to be an abandonment of the evolutionary point of view that has shaped biology since 1859 at a point where it has become more achievable.

The paraphyly problem at genus level is the result of three incompatible things: (1) the desire to recognise natural groups or clades as genera, (2) the desire to recognise monophyletic groups, and (3) the present Botanical Code of Nomenclature's system of exclusive ranked naming, where a species can belong to only one genus. To avoid recognition of non-monophyletic genera, the solution forced on cladists is not to recognise as genera the many distinctive and monophyletic groups that arise from within other genera, or to recognise any such group as a genus but to break up the paraphyletic group that remains into a number of genera. Both of these solutions is unsatisfactory for the reason that groups are being named or not named to satisfy nomenclatural requirements.

In a rankless system of nomenclature, the problem of paraphyly is avoided as it is possible to name both a new distinctive clade that has radiated from within an existing one, and the existing one. This is one of the main points in favour of a change to a rankless system of naming such as the Phylocode of Cantino & de Queiroz (2001). A rankless system of naming would solve the paraphyly problem for the large number of cladist taxonomists who wish to recognise monophyletic groups only. It would not offer any advantage to the also large number of non-cladistic taxonomists for whom the problem of paraphyly does not exist, and who wish to recognise genera of the form 'group A with the exclusion of the species of group B' where group B is nested within group A.

My own preference is for a code of nomenclature which allows expression of phylogenetic relationships and allows adoption of monophyletic groups. I believe that the adoption of a rankless system of naming is the only way to achieve this.

The species concept

There is little disagreement among taxonomists that, as Waddington (1962) said "it is an empirical fact that living organisms do not vary continuously over the whole range, but

that they fall into more or less well defined groups which are commonly called species". The problem is that these groups form a hierarchy and that what we call species lie in an intermediate position in this hierarchy. The debate over the species concept is as to whether there is some conceptual basis for regarding species as a special category in this hierarchy and how this conceptual basis can be applied. The biological species concept is such a conceptual basis.

The validity of the biological species concept rests on the hypothesis that gene flow within and between populations of a species maintains its uniformity. If true, it is part of the explanation of the discontinuity mentioned by Waddington. (The other part of the explanation is that extinction creates gaps between species and groups of species.) This discontinuity occurs at only one point in any hierarchy of organisms, the point at which a sterility barrier arises between branches in a dividing lineage. It offers the only possibility of a non-arbitrary rank in the taxonomic hierarchy. The phylogenetic species concept that uses the boundary between reticulate and non-reticulate relationships between lineages to mark the level of species (Judd et al. 1999) is a re-expression of the same explanation. The ecological species concept fails to explain why in an environment that grades in most characteristics that affect plants such as soil moisture and soil fertility, there should be biological discontinuities.

The biological species concept cannot be applied to allopatric taxa that may make up the majority of cases in a group. When organisms disperse long distances and establish new populations, these new populations diverge in time from the parent population. All degrees of difference will exist in this situation, and will correspond to what we would call subspecies, species and given enough time, genus or family. On one island in an island chain, Waddington's statement may be true. But when we look along the chain, Waddington's statement does not apply, and how we nominate what are to be species in this situation is arbitrary. Ability to hybridise artificially could be used as a criterion, but would be an artificial one. In recently radiated groups, allopatric taxon pairs will often constitute the majority, since speciation, it is agreed, requires geographic isolation in most cases. It is this difficulty that means that most plant taxonomists still recognise what Davis & Heywood (1963) call the "morphological-geographical" species at the same time as it is true that "The biological species concept is the one held conceptually by most systematists at the present time" (Stuessy 1985).

Mayr et al. (1953, p. 103) recommend the rule of thumb that allopatric species pairs should show the number of morphological differences between sympatric species pairs: "Since direct proof [of ability or lack of ability to interbreed between allopatric

pairs] is unavailable, it becomes necessary to decide the status of isolated populations by inference. Several types of evidence are available. All of these are based on the observation that reproductive isolation is correlated with a certain amount of morphological difference which is fairly constant in a given taxonomic group." Mayr et al. provide no evidence for their assertion. We know that it is not always the case, since reproductively isolated species can result from a change in ploidy level with hardly any morphological differences.

Some authors maintain that despite this, it is possible objectively to discern species just on the basis of morphology and distribution. Davis & Heywood (1963) stated that the success of the morphological-geographic manner of delimiting species "was largely due to the fact that the groups it recognised very often correspond in nature to breeding populations". This is not quite correct, as Rieseberg & Burke (2001) point out that species are generally composed of a number of populations between which there is a low level of gene flow. Davis & Heywood do not face the fact that in allopatric taxa, there is no way of delimiting species that is not merely the application of an arbitrary rule.

The doubts raised by Raven about the extent of gene flow and whether it is a sufficient explanation of uniformity of species have been widely accepted among botanists. The variability often recorded in widespread New Zealand alpine herbaceous species (e.g., in *Celmisia*, *Chionochloa*, *Epilobium*, *Leptinella*, and *Ranunculus*) gives support to the idea that gene flow is indeed limited, but the arguments of Rieseberg & Burke (2001) make it seem possible that these species are being maintained by low levels of gene flow over long periods. To design experiments to distinguish the effects of low levels of gene flow between populations and the effects of uniformity of environment would not be easy, and to decide between these competing hypotheses is very difficult.

Raven & Raven (1976) were able to provide a classification for New Zealand *Epilobium* despite their belief that the species were not coherent as a result of interbreeding. They state that those species that are found in the most distinctive ecological situations (such as the scree species *E. pycnostachyum* and *E. forbesii*) are also the most sharply distinct species on morphological grounds, while the converse was also true: the more widespread and less specialised species were the most difficult to deal with taxonomically.

The genus *Gentianella*

Sequencing the ITS DNA regions established that the New Zealand gentians belong within *Gentianella* rather than *Gentiana*. Hagen & Kadereit's (2001) world-wide DNA ITS and matK survey, done concurrently with this revision, has shown that New Zealand *Gentianella* had its origin in South America, and that the Southern Hemisphere short tube gentians could possibly be split from *Gentianella* section *Amarella*, but such a split should not be made at present, and that the Australasian species of *Gentianella* should not be separated from the South American species. As explained in detail in the Introduction, the uncertainty over the relationship of the efimbriate species of *Gentianella* to the rest of the genus makes the segregation of the Australasian species and most of the South American species into a separate genus unjustifiable at present. As a consequence, I am rejecting the recently published name *Chionogentias* (Adams 1995) made for the Australian and New Zealand gentian species.

The species concept used in this revision

In this revision decisions of what species to recognise are based primarily on evidence from morphological characters, with extensive use made of distributional evidence, particularly sympatry of sibling species and subspecies and geographic patterns of variation.

Subspecies rank is used for the following reasons: firstly, almost universal use of the rank for geographically and morphologically distinct variants in the New Zealand vascular plant flora in the last 20 years (e.g., Edgar 1986 in *Poa*, Sykes 1992 in *Macropiper*), and secondly, to maintain uniformity with Adams' (1995) Australian revision and Gillett's North American revision of 1957, both of which use subspecies rank only. The rank of variety is the only infraspecific one that had been used previously in the New Zealand gentians. However, consistency with this precedent did not seem a strong reason to use the rank of variety, as only one pre-existing variety in New Zealand *Gentianella* needed to be maintained at infraspecific rank. However, in just one case, I have maintained an already existing variety, *G. montana* var. *stolonifera* because it is defined by a single character, and this difference is not consistently present in the variety. In the field, this taxon looks very distinct (although extremely variable over its range) and detailed molecular studies are probably the best way to resolve its status.

New Zealand *Gentianella* has a strong tendency to develop geographic variation that probably reflects very limited gene flow between populations. Not to use an infraspecific rank often would either necessitate no recognition of distinctive geographic

entities, or would involve the creation of a species-level classification that would present practical difficulties to users.

The circumstance in which I have recognised subspecies has been where there are allopatric populations that were distinct for a limited number of mainly quantitative characters, particularly where these overlap in their ranges but differ in their means. Such a level of difference indicates recent differentiation. It may be impossible to assign all specimens to a subspecies. This is the case for the two subspecies I have recognised in *G. corymbifera*, and *G. montana* var. *stolonifera* where its only defining feature, the presence of stolons is not present in all plants of var. *stolonifera*, while plants of *G. montana* s. s. occasionally have stolons.

Lack of evidence from breeding experiments led me to rely on numbers of morphological differences between allopatric sibling taxa in making decisions on what should be regarded as species versus subspecies. Correct identification of the nearest relative of a sibling taxon is in my view critical to this process. In my view, the distinction between allopatric species and subspecies in the absence of results from artificial crosses or detailed molecular evidence at the population level can often be an arbitrary one. In the case of allopatric sibling taxa, I have assessed their level of difference, often expressed in tables (Tables 10, 11, 16, 18, 19, 20, 25, 26, 38, 42, and 49) taken in combination with geographic range to assess how widespread the taxon is and how isolated it is, and knowledge of habitat, to assess whether it occupies a distinctive ecological niche or has adapted to unusual edaphic conditions. Where I have recognised a species, there were usually more than six differences separating it from its nearest sibling taxon. This includes quantitative characters where there may have been some overlap in ranges. Subspecies often showed only four or five such differences, often with overlapping ranges in quantitative characters. These degrees of difference are comparable to those used by Adams (1995) who recognised two sibling species *G. pleurogynoides* and *G. brevisepala* which differed in eight characters which were all quantitative but with no overlap in ranges. There are five differences between two subspecies of *G. diemensis* subsp. *plantaginea* and *G. diemensis* s. s., with overlap in ranges of quantitative characters. Gillett (1957) listed four differences between *Gentianella quinquefolia* ssp. *occidentalis* and *G. quinquefolia* s. s. with no overlap in the ranges of the three quantitative differences. Klackenberg (1985) gave four differences, all quantitative, between two sympatric Gentianaceae species, *Exacum grande* and *E. hamiltonii*, two of which involved overlapping ranges. Klackenberg did not recognise any subspecies.

In the *G. bellidifolia* group, sympatry of sibling taxa to the parental species, *G. bellidifolia*, necessitated a different approach. In this group, I recognised species if they were sympatric and no intermediates were visible, despite only minor morphological differences. In the case of *G. decumbens*, my perception of it as a species was strongly influenced by its distribution along the full length of the Arthur Range, but absent from the large block of marble substrate at Mt Arthur and the Twins.

In *G. corymbifera* I recognised subspecies that were overlapping in distribution but separated in altitude. It could be argued that *G. serotina* and *G. bellidifolia* should be treated in the same way. Further field observations in Otago and Southland and molecular evidence at population level are needed to understand the relationship between the two there.

It is sometimes stated that the degree of difference between pairs of sympatric species be used as a guide for deciding on the rank of allopatric taxa (e.g., Mayr 1942). While pairs of sympatric species such as *G. impressinervia* and *G. montana* could be used in this way, the *G. bellidifolia* group has sympatric pairs of species which are the least morphologically distinct of any pairs and could not be used as such a guide.

Review of taxonomic decisions made

The G. divisa group

Examination of this group revealed one unnamed species, *G. luteoalba*, and one unnamed subspecies, *G. corymbifera* ssp. *gracilis*. On grounds of its weak morphological distinctness, I decided that the narrow leaved form of *G. corymbifera* should be a subspecies. Only at one site, near Lake Ohau did I see the two close to each other, but still separated. A closer examination along the Ohau Range would assist in deciding whether these two subspecies meet and how they behave where they meet. Attempts at hybridising the two by cross pollination in the field and bagging flowers would be useful, and would avoid the problems of attempting to raise both to flower at the same time in the glasshouse. The Ohau site would be convenient for such an experiment.

G. divisa var. *magnifica* was also distinct enough to warrant being regarded as a species, although it is composed of two populations that are c. 50 km distance from each other. This situation can be seen elsewhere, for instance in *Epilobium forbesii*, also a species confined to black argillite scree habitat with its main population on peaks from the upper Wairau Valley to Mt Terako, and an isolated population 200 km to the south in Mid Canterbury. *G. magnifica* may occur on other mountains with black argillite

scree. It may occur on Dillon Cone (G. Spearpoint, pers. comm., no voucher). Department of Conservation staff did field work on the northern end of the Rachel Range during the summer of 1999/2000 but did not find any new sites for the species (C. Jones, pers. comm.).

I decided not to recognise the Nelson and Marlborough populations of *G. corymbifera* as a separate subspecies of *G. corymbifera* for the reason that there were too few differences. However, the Principal Components Analysis showed the Nelson and Marlborough specimens to be distinct in being, on average, larger than those of Canterbury and Otago. A geographic break exists between populations in Canterbury and in Nelson, so that even if it is difficult to provide a workable key to the subspecies, there would be no problem in assigning specimens to a Nelson – Marlborough subspecies. This is in contrast to the situation in *G. corymbifera* ssp. *gracilis* where the overlap in range means that morphological differences must be examined carefully in most cases to determine specimens.

The *G. divisa* group appears to be old enough to have developed some very distinct species, particular *G. filipes*, which is well separated geographically from its nearest relatives. The group's evolutionary history is easier to trace than in some other groups in New Zealand *Gentianella*. I have been unable to positively determine the group's affinities to other groups in New Zealand *Gentianella*, and this question would be one worth resolving with DNA sequences.

The G. montana group

While *G. vernicosa* and *G. impressinervia* are very distinct, the *G. montana* species complex (including *G. patula*) was a very difficult one to analyse, and it is possible that within *G. montana* ssp. *montana* there exists an unrecognised species that has a similar distribution as *G. montana* but a wetter habitat. This is the sometimes stoloniferous form of *G. montana* with orbicular leaves and a very narrow petiole that occurs in wet sites between South Westland and Nelson (outside of the range of *G. montana* var. *stolonifera*). This form is abundant on the Goulard Downs. In the field I was convinced that this was a species that I called *G. "South Island patula"* (*G. "North Island patula"* being *G. montana* ssp. *ionostigma*). However, some specimens I collected under this name are *G. bellidifolia*, having only lateral flowering stems, and I doubt my earlier judgement of the distinctness of *G. "South Island patula"*. The presence or absence of a terminal leaf rosette that does not have a flowering stem is very difficult to see on most pressed specimens, making some specimens of *G. bellidifolia* and this wetland form of

G. montana difficult to determine. To resolve this question, it would be helpful to do further field work or experiments involving transplanting *G. montana* between dry and wet sites.

The G. spenceri group

For most of the duration of the study, I considered that the group had its origin from *G. montana* in South Westland and that an undifferentiated form similar to both *G. spenceri* and *G. tenuifolia* was present in South and Central Westland that I called *G. "subalpina"*. Examination of Central and South Westland specimens convinced me that this was not so, and that Central Westland specimens belong to *G. spenceri* and perhaps *G. tenuifolia*. South Westland specimens are more difficult to place.

G. chathamica ssp. *nemorosa* of the North Island appears to be most closely related to *G. chathamica*. The southern limit of *G. chathamica* ssp. *nemorosa* is in the Ruahines and so observes the lower North Island floristic gap noted by Rogers (1989). Rogers believes that many disjunctions in the vascular flora of North and South Island match the extent of the marine transgression that inundated the lower North Island in the early Pliocene. It seems unlikely that the speciation of *G. chathamica* dates to the Pliocene (2–6 Ma). Rogers also attributes absences from the Tararua Range to a lack of some habitats in the very tectonically active Tararua Range. This is a more credible interpretation for *G. chathamica*'s distribution. In uniting *G. chathamica* ssp. *chathamica* and *G. chathamica* ssp. *nemorosa* as subspecies of the same species, there is an implicit claim that *G. chathamica* had its origin in North Island *G. spenceri*-like plants, rather than South Island *G. spenceri*. The phenetic comparisons done here (PCA and comparison of means) only present evidence of similarity. The relationships posited are likely to be true, but are not certain.

This group is the only one that has no representatives in Southland. Consequently its origin is something of a mystery to me, but may be from a *G. matthewsii*-like ancestor in South Westland.

The G. grisebachii group

There are two very distinct species in this group, *G. lineata* and *G. gibbsii*. *G. gibbsii* may be the result of speciation from *G. grisebachii* on Stewart Island during a period of isolation. Alternatively, *G. gibbsii* has become a high altitude form of *G. grisebachii*. The *G. grisebachii* complex shows geographic and habitat variation that is very difficult to deal with taxonomically. My solution to this was to recognise only one species for

the reason that I could see no way of providing a separation between the two which would work for a majority of specimens and that would be anything but an arbitrary split using one character. No correlation of characters allowed a split using more than one character.

The G. bellidifolia group

Examination of this group showed that all taxa are very close morphologically. The differences between *G. amabilis* and *G. bellidifolia* are very slight. The two species are very closely sympatric and flower simultaneously. They must therefore have an internal reproductive isolation mechanism, showing that it is possible for species, at least in this group, to exist with few morphological differences.

This sympatry of species with very minor differences is a feature of the *G. bellidifolia* group, although this sympatry is not as well established in other cases as it is in the case of *G. amabilis* and *G. bellidifolia*. *G. decumbens* occupies drier and higher altitude habitat than *G. bellidifolia* and is easily recognised by its habit and size, but it lacks floral differences except for the nectaries that are usually further from the corolla base than in *G. bellidifolia*. The geographic range of *G. decumbens* falls entirely within that of *G. bellidifolia*, but the habitats are usually well separated, by some hundreds of metres.

The same obtains for *G. serotina*, a species with a wide overlap in range with *G. bellidifolia*, but found in drier, usually lower altitude habitats. I have not seen *G. serotina* and *G. bellidifolia* growing together in the way *G. amabilis* and *G. bellidifolia* do on the Old Man Range, and so the degree of reproductive isolation of the two is unknown. Difficulties with assigning specimens from the broad ridges of the Old Man Range and Hector Mountains to one or other species suggest that the two may not constitute two biological species in this part of Otago.

G. bellidifolia is a widespread species that is variable in size. A size variant with a distinct geographic range and substrate, *G. angustifolia*, appears to be a biological species in the way that *G. decumbens* is, and with almost the same range, although different habitat.

This group is unusual in the New Zealand gentians in having all its segregate species overlapping in geographic range with the parental species *G. bellidifolia*. It shares this with the *G. montana* group, but that group differs in having at least two very distinct species from the widespread *G. montana*.

The *G. bellidifolia* group would be a promising subject for a detailed study on

sympatric speciation.

The G. astonii group

In this group of six taxa, I initially worked with the hypothesis that they should be recognised as separate species. Examination of the morphological differences between them, particularly the Marlborough taxa for which there was a greater abundance of specimens, convinced me that this view could not be sustained, as examination of more material lessened the apparent quantitative differences between the taxa. Some qualitative differences were also found, particular in the shape of the nectary, but as more material was examined, the flap covering the base of the nectary and its toothings were found to be more variable than appeared initially.

Because all six taxa occur on eastern South Island lowland limestone outcrops, they are adapted to summer dryness. All six have responded to this by being late flowering relative to other New Zealand *Gentianella* species, with their peak flowering in April and May, but in the case of *G. astonii* ssp. *arduana*, flowering as late as October. They also share some morphological features, notably the bushy form resulting from repeated branching, the black stems (this feature shared with many other New Zealand *Gentianella* species) and the small, narrowly elliptical to linear leaves, that are not tinted by secondary pigments. All subspecies in the *G. astonii* group except *G. astonii* ssp. *astonii* share the feature of having serrulate leaf and calyx margins. *G. astonii* ssp. *astonii* has one other autapomorphy not possessed by the other subspecies of the *G. astonii* group: smooth calyx and leaf margins. It shares with *G. astonii* ssp. *arduana* the synapomorphy of a deep nectary pocket with a toothed margin, a feature not seen in other species of New Zealand *Gentianella*. *G. astonii* ssp. *arduana* and *G. calcis* ssp. *waipara* share finely serrulate corolla lobe margins.

The subspecies of *G. calcis* share the feature of having recurved and keeled leaves. *G. calcis* ssp. *taiko* is the most distinct of these four subspecies, in its small flower parts, its leaves that are long with an expanded blade and distinct petiole, a more pocket-shaped nectary, and corolla sinus hairs that are dense and very strongly curled. *G. calcis* ssp. *manahune* is the only subspecies of the *G. astonii* group with coloured corolla veins.

Although the relationships between the subspecies are not completely clear, a trend in morphology is apparent on a north-south axis. The most derived species appear to be in Marlborough and the least derived in South Canterbury and Otago. *G. calcis* ssp. *calcis* is closer to *G. serotina* in appearance than it is to *G. astonii*. All subspecies of *G.*

astonii and *G. calcis* have autapomorphies which set them apart from their geographically close relatives. It can be speculated that the group has dispersed from south to north, dispersing from one Tertiary limestone outcrop to the next, missing some major limestone outcrops such as those at Mount Somers and Castle Hill basin. The peculiar autapomorphies of each subspecies, such as loss of anther pigment and the toothed nectary flaps, may have resulted from the founder effect.

All members of *G. astonii* and *G. calcis* are allopatric and are isolated by their preferred limestone substrate. I have made them subspecies on grounds of the degree of their morphological distinctness, which from one to the next is not great. Only small numbers of specimens were available for compiling descriptions of the less common subspecies.

Only the Marlborough subspecies of *G. astonii* are close enough for to hybridise naturally. Examination of the area between the Chalk Range and the Waima catchment is needed to establish the exact geographic distance between *G. astonii* ssp. *astonii* and ssp. *arduana* and whether hybridisation has occurred there.

Biogeography

Gentianella is unique in the flora of the New Zealand Subantarctic Islands in having different sibling species on each of the three largest islands, *G. cerina* and *G. concinna* on the Auckland Islands, *G. antarctica* on Campbell Island, and *G. antipoda* on the Antipodes Islands. The reason for this seems likely to have been that they have dispersed between the islands infrequently enough and have evolved rapidly enough to differentiate on each island or cluster of islands. It is difficult to explain how *G. concinna* and *G. cerina* of the Auckland Islands could have speciated from a common ancestor sympatrically in view of the size of these islands and the apparent lack of habitat separation between the two. The situation in *Gentianella* can be compared with that in *Anisotome*. *Anisotome latifolia* and *A. antipoda* are both on the Auckland Islands and Campbell Island, and *A. antipoda* is also on the Antipodes Islands (Dawson 1961). If *A. latifolia* and *A. antipoda* are sibling species, it seem unlikely they speciated on a single island and then dispersed to the other islands. Allopatric speciation could occur if one species on the Auckland Islands dispersed to Campbell Island or the Antipodes Islands, speciated in isolation, and then dispersed back to the Auckland Islands. No such explanation can be suggested in *Gentianella* without supposing extinction of *G. cerina* or *G. concinna* on Campbell Island or the Antipodes Islands.

The species that make up the *G. saxosa* group show a trend from *G. saxosa* to *G.*

antipoda in ten characters (Table 14). Without knowing the immediate outgroup to the *G. saxosa* group it is not possible to be sure of whether *G. saxosa* or *G. antipoda* is basal in the group. The evidence of a unique synapomorphy at nucleotide position 21 on the ITS sequences and the synapomorphies of small floral dimensions and small number of ovules per ovary shared only by *G. antipoda* and *G. antarctica* in the *G. saxosa* group suggests that these Subantarctic gentians are not basal in the *G. saxosa* group and that *G. saxosa* is the best candidate for the basal species of the group. If this is accepted, it is unlikely that the New Zealand gentians arrived from South America via the Subantarctic Islands, although this does not rule out a dispersal from South America to the New Zealand mainland via Antarctica that bypassed the Subantarctic Islands, or extinction and recolonisation of the Subantarctic Islands during the Pleistocene.

An outline of the history of the radiation of the genus in New Zealand can be constructed based on the intuitive phylogeny presented in Fig. 37. This history is admitted to be highly conjectural. I believe that after arrival in New Zealand in Southland or Otago, there was an initial radiation in those provinces into about four species: the basal species of each of the *G. saxosa*, *G. bellidifolia*, *G. montana*, and *G. divisa* groups. While *G. saxosa* is a strictly coastal species, the other groups are entirely montane to alpine and this initial radiation was induced by the availability of alpine habitats created by the Kaikoura orogeny. At about the time of this initial radiation, the ancestor of *G. saxosa* dispersed to the Subantarctic Islands and radiated there into four species, and to Westland. The ancestor of *G. divisa* possibly speciated into *G. corymbifera* and *G. divisa* in Otago, either before or after dispersal north of what became *G. luteoalba* and *G. filipes*. The ancestor of *G. montana* probably gave rise to the ancestor of *G. grisebachii* in Southland or Otago. The ancestors of *G. montana* and *G. bellidifolia* perhaps spread northwards up the South Island, and on reaching Westland or Nelson gave rise to the ancestor of the *G. spenceri* group. A radiation occurred in Nelson of the *G. spenceri* ancestor into three species there. *G. bellidifolia*, on reaching Nelson, gave rise to *G. angustifolia* and *G. decumbens*. In Otago, *G. bellidifolia* may have given rise to *G. amabilis* and *G. serotina*. Either *G. bellidifolia* or *G. serotina* or their ancestor gave rise to *G. calcis* in Otago, which progressed northwards by saltation towards Marlborough using limestone outcrops as stepping stones.

Relatively recently, four gentian species dispersed from the South Island to the North Island: *G. grisebachii*, *G. bellidifolia*, and *G. montana*. Uplift of the North Island mountains occurred only c. 0.2 Ma (Ghani 1978), much later than the South Island mountains. This is reflected in the less-strongly differentiated North Island taxa

suggesting that the gentians established in the North Island only after montane habitats became available. A relationship between *G. chathamica* s. s. and *G. chathamica* ssp. *nemorosa* is posited on the basis of their similarity, but this similarity does not make it possible to say whether a *G. spenceri* ancestor dispersed from the South Island to the Chatham Islands, and a descendant dispersed to the North Island, or the route was from the South Island to the North Island and thence to the Chatham Islands.

Thus an initial radiation in the southern South Island into four species of montane or alpine tussockland preceded range extension and saltational dispersal northwards into Nelson where a second radiation occurred that was caused mainly by a combination of isolation and specific substrate conditions, perhaps assisted by other factors. At about the same time as this Nelson radiation, further radiation continued in Southland and Otago in the *G. grisebachii* and *G. bellidifolia* groups. Probably following both of these radiations, dispersal to the North Island occurred, allowing only weak speciation there.

In both the early southern radiation and in the later Nelson radiation, some species adapted to alpine tussockland and scree habitats, but other species adapted to montane forest habitats and forest-free valley grasslands.

New Zealand *Gentianella* has its origin in South America, but it is not known from where in South America the plants dispersed. As most of the diversity is in the northern Andes (Ecuador, Peru, and Bolivia), and some species I examined from there are very similar to New Zealand species (e.g., *G. foliosa*), it seems likely that one dispersal from that region was involved. Investigation of South American *Gentianella* using a more variable DNA region than ITS or matK offers the best chance of finding the place of origin in South America of the New Zealand gentians and rooting its phylogeny. A single dispersal from New Zealand has probably given rise to all the Australian species, and further sequencing of ITS DNA could confirm this. These dispersal events have taken place despite the fact that the seeds have no special adaptations to dispersal. The arrival of *Gentianella* in South America and Australasia is late Tertiary or early Quaternary. Hagen & Kadereit (2001) used the first fossil pollen record in South America of 1.6 Ma (from van der Hammen 1979) as their latest possible time of arrival in South America, but speculated that the arrival of *Gentianella* in the Andes may have coincided with their uplift 3 Ma.

Origins and timing of evolution

What can be concluded about the important issues of biogeography from this revision?

The New Zealand species had a South American origin. The Australian species probably had their origin in New Zealand species. An approximate time of arrival of *Gentianella* in South America and New Zealand was estimated by Hagen & Kadereit (2001) as two Ma. From this an approximate rate of speciation can be derived of one cycle every 400 000 years. If it is accepted that the *G. saxosa* group is basal to New Zealand *Gentianella*, and that *G. saxosa* is the most basal species in this group, then a "landing place" in New Zealand can be hypothesised in coastal Southland. This is consistent with the evidence that Southland and Otago were an initial area of radiation that preceded the northern South Island speciation events. A scenario for the evolution of the group in New Zealand involves two types of processes: range extension of some widespread species such as *G. montana*, *G. bellidifolia* and *G. grisebachii* and geographic variants within these widespread species becoming quite distinct. Secondly, speciation events followed long distance dispersal of seed to new localities. In the northern South Island, speciation in several cases resulted from special soil types, while in others it resulted from distinctive habitat types such as alpine fellfields and screes.

The DNA evidence presented in the results does not allow the conclusion that the Australian species of *Gentianella* had a New Zealand ancestor, but morphological evidence indicates that this is likely. Serrate calyx lobe margins in the Australian species indicate they are derived from the *G. bellidifolia* group. The presence of terminal flowering stems in the Australian species contradicts this and suggest they branch further back in the tree than the *G. bellidifolia* group.

Rates of speciation are calculated as the time since the estimated arrival of an ancestor or the uplift of an island group divided by the number of species that have radiated from that arrival. This is misleading in that it suggests that the rate gives the time between speciation events. The method of calculating the rate of speciation should be measured as follows:

$$\text{rate of speciation} = \text{time since divergence} / \log_2 (\text{number of species})$$

This is based on the neutral assumption that speciation involves one species becoming two and that for a recent group extinction is not a factor, and the number of species will increase in a geometric series of 1, 2, 4, 8, 16, 32 etc. If a phylogenetic tree is available, this neutral assumption can be improved on by counting the number of speciation cycles. For South American gentians this leads to a rate of one cycle of speciation per 400 000 years using Hagen & Kadereit's (2001) dates. For New Zealand, one cycle of speciation

per 420 000 years, again using Hagen & Kadereit's dates. These are very different figures from those calculated by Hagen & Kadereit who divided the number of species into the number of years to obtain their rate of speciation (one species per 17 000 years for South American *Gentianella*). Their rate assumes that only one speciation event is happening at any time, an unreasonable assumption. The New Zealand rate of speciation is half the rate that can be calculated from the dates and numbers of species given by Lowrey (1995) for Hawaiian *Tetramolopium* where 11 species evolved in c. 650 000 years, giving one cycle of speciation every 191 000 years. Stuessy et al. (1998) give a rate of speciation in *Dendroseris* on the Juan Fernandez Islands of 1 species per 364 000 years (11 species have differentiated in 4 million years). This equates to 1.16 million years per speciation cycle, a much slower rate than that estimated by Lowrey, or those I have derived from the estimates of Hagen & Kadereit. A factor not considered in the island examples of Lowrey and Stuessy et al. is the time between the appearance of an island group and the arrival of the ancestor of the species of *Tetramolopium* and *Dendroseris* respectively. This is likely to be significant, since if it was not, the conditions of isolation that allow speciation to proceed would not exist.

In New Zealand, the first Gentianaceae pollen is recorded from the late Miocene, c. 11 Ma (D. Mildenhall pers. comm.) at a site in Northland, but Mildenhall says of this record, and another similar record from the middle Pliocene from Westland, "I do not think that they are like any modern New Zealand gentian." The first New Zealand pollen grains that resemble those of *Gentianella* are from a relatively large number of sites of Nukumaruan age (2.6–1.6 Ma), and it is not possible to be more precise over their dates within this million year period (D. Mildenhall pers. comm.). This sets the latest possible arrival date of *Gentianella* in New Zealand as simultaneous with its latest possible arrival date in South America, while the earliest arrival date of 2.6 Ma is consistent with Hagen & Kadereit's speculation that *Gentianella* may have arrived in the Andes 3 Ma.

Within New Zealand, a southern South Island place of origin and initial radiation is indicated by a combination of phylogeny and geographic distribution of species. Northward range extension can be seen in a number of species and there is a second centre of speciation in Nelson and Marlborough. Only four *Gentianella* species have dispersed to the North Island from the South Island and this has happened recently enough for only one of the four to have diverged sufficiently to be regarded as a species. There have also been a number of southward dispersals to the Subantarctic Islands, but the earliest of these probably occurred before the South Island radiation, as four very

distinct species occur there. The *G. saxosa* group appear to be the oldest group in New Zealand *Gentianella*, but the Campbell and Auckland Island species are the most derived in that group.

Speciation in the New Zealand gentians has most often followed dispersal over a distance that has effectively isolated the new population. This is particularly obvious in the case of gentians that are endemic to Stewart Island, the Chatham Islands, and the Subantarctic Islands, but can also be seen in the South Island. The second most common cause of speciation has been adaptation to substrate types, marble, limestone, granite, and ultramafic rock and their derived soils. In common with other herbaceous genera in New Zealand, a number of species have adapted to new habitats in the drier South Island mountains, e.g., those of scree and fellfield. In some cases, both isolation and a new substrate type have jointly led to speciation.

Australian species of *Gentianella* are generally monocarpic, and most (e.g., *G. muelleriana* and *G. cunninghamii*) have the appearance of *G. matthewsii*. They are tall (c. 30 cm) and erect, slender, lack a distinct leaf rosette when flowering, have elongating pedicels, and coloured corolla veins. *G. diemensis* is different from most of the Australian species in having the appearance of New Zealand's *G. corymbifera*: it has a stout taproot, wide-petioled leaves, and a short but much branching inflorescence. However it is polycarpic, while *G. corymbifera* is usually biennial. The existence of these two types suggests two dispersals from New Zealand to Australia. However, all Australian species I examined have the synapomorphy of serrated calyx lobe margins in common with *G. serotina* and *G. astonii*, and *G. diemensis* shares with three other Australian species several synapomorphies in its ITS DNA sequences, suggesting a single dispersal. If a single dispersal of a *G. serotina*-like ancestor has given rise to all the Australian species, the Australian species have become mostly monocarpic from a polycarpic ancestor, since *G. serotina* is polycarpic.

Notable in the Australian species are the large number of ovules, 49–60 per ovary, numbers matched by only a few of the larger polycarpic New Zealand species (*G. paparoensis*, *G. stellata*, *G. montana*, and *G. serotina*). Some New Zealand species show the opposite extreme, 3–9 ovules per ovary in *G. antipoda*. This result of a selfing syndrome is shared by *G. antipoda*, *G. antarctica*, *G. lilliputiana* and some populations of *G. spenceri*. A better pollinating fauna may account for this feature of the Australian species, although it is at odds with the small anthers that some Australian species have, a feature seen in New Zealand only in *G. chathamica* ssp. *chathamica*.

The corollae of most Australian species have coloured veins, the veins described

by Adams (1995) as grey-violet or grey-green to grey-violet. This coloration is seen in New Zealand in *G. grisebachii* and *G. astonii*, but the predominant colour in the New Zealand flowers is crimson to purple.

Modes of speciation in New Zealand *Gentianella*

The modes of speciation in the New Zealand gentians can be hypothesised from their relationships and distribution. What follows is also speculative, as is based on the conjectural history above.

The main pre-condition for speciation appears to have been long distance dispersal, that is, dispersal far enough to isolate the newly established population from its parent population. Ocean barriers have been the main cause of this, but isolation within the South Island has also been responsible for speciation.

There are three groups of species that demonstrate long distance dispersals to offshore and outlying islands: (1) From New Zealand's South Island to the Subantarctic Islands, over distances of 460–820 km. (2) A dispersal from the North Island to the Chatham Islands, or the reverse, a distance of 800 km, relatively recently as shown by the close relationship of *G. chathamica* to its subspecies in the North Island. (3) The dispersal of a *G. grisebachii* ancestor to Stewart Island has possibly given rise to *G. gibbsii*, but it is possible that this occurred at a time when Foveaux Strait was bridged by land, as it was during the last glaciation (Fleming 1979).

Four dispersal events from the South Island to the North Island have probably occurred, possibly at about the same time, and probably after much of the Nelson radiation occurred. (1) *G. spenceri* has either dispersed to the North Island and speciated to become *G. chathamica*, or has dispersed to the Chatham Islands and from there dispersed, as *G. chathamica*, to the North Island. Its absence in the Tararua Range may be due to a lack of suitable habitat at some time in the recent past. (2) *G. montana* has dispersed to the North Island and is present in the North Island from the Tararua Range to Mt Hikurangi, where it has diverged enough to be recognised as a subspecies. (3) *G. bellidifolia* has dispersed to the North Island and has changed little. (4) *G. grisebachii* has dispersed to the North Island and shows similar variation there to that seen in the South Island, but has extended its habitat range to open forest and forest margins.

Within the South Island, several dispersal events followed by isolation seem to have occurred: (1) A dispersal event of *G. saxosa* from Southland to Charleston followed by the speciation in isolation of *G. scopulorum*. A dispersal event rather than

extinction of *G. saxosa* from the Westland coast is hypothesised because *G. saxosa* has its northern limit at Breaksea Island and is absent from suitable habitat along most of the coastline of Fiordland. (2) Dispersal from Canterbury to Marlborough and Nelson of *G. divisa* which has resulted in the speciation of *G. magnifica*, *G. filipes* and *G. luteoalba*. Their varying degrees of distinctness from *G. divisa* may reflect the length of time since each dispersed.

No firm hypothesis has been formulated as to how *G. vernicosa* and *G. impressinervia* speciated from the ancestor of *G. montana*. It is possible that they speciated in isolation after a dispersal event a time when *G. montana* was not present in Westland and Nelson.

Rock and soil types appear to have been the main driver for speciation in several cases, either with or without isolation: (1) The limestone outcrops of the eastern South Island have provided a distinctive habitat and effective isolation. Five dispersal events from outcrops in the south to those in the north are required to explain the six limestone taxa belonging to *G. astonii* and *G. calcis*. (2) Ultramafic rock and soils derived from it have caused *G. stellata* to speciate from *G. tenuifolia*. This is a particularly clear case of parapatric speciation of an edaphic endemic. (3) The marble of the Arthur Range has caused *G. angustifolia* to speciate from *G. bellidifolia*. This is probably another case of parapatric speciation of an edaphic endemic, although soils derived from marble are less extreme in their chemistry than those derived from dunite. The marble may also have been a factor in the speciation of *G. filipes*. (4) Granite fellfield has been a factor in the differentiation of *G. luteoalba*. (5) Fine argillite scree has been a cause of speciation of *Gentianella magnifica*, assisted by isolation. These last four cases are in Nelson and Marlborough. (6) *G. decumbens* is mostly found on sparsely vegetated summit fellfields while its parent species, *G. bellidifolia*, is found in moist peat soils in the same vicinity. This may be a case of speciation without isolation, but this would probably be impossible to prove.

The gentian species in New Zealand are often well matched to the height of the vegetation they are found in. A number of the tallest species, *G. montana*, *G. impressinervia*, and *G. corymbifera* are found in *Chionochloa pallens* tussockland. The smallest species grow in short grasslands, herbfields or cushionfields, e.g., *G. filipes*, *G. vernicosa*, *G. lineata*, and *G. amabilis*. Success in matching the height of the various *Chionochloa* species has probably been a factor in the adaptive radiation of the New Zealand gentians.

Three cases involve an altitude separation with a barrier between valley floors

and the alpine zone probably provided by continuous forest on the mountain slopes below treeline. (1) *G. corymbifera* subsp. *corymbifera* and subsp. *gracilis* have been isolated in this way for long enough to be distinct enough to be recognised as subspecies. (2) *G. serotina* has speciated from *G. bellidifolia* in the same way. (3) *G. corymbifera* in North Canterbury has also been separated in this way, but the only differences between the alpine and valley floor populations are a difference in anther colour, plant size, and the number of flowering stems. To my knowledge, this mode of speciation has not been hypothesised in New Zealand botanical literature, although Burrows (1964) noted that some species in Canterbury show a disjunction between the alpine zone and valley floor.

In two cases, there appears to have been fragmentation of populations with subsequent speciation, and both involve granite versus greywacke substrates that may have been an influence. Soils derived from granite are of lower fertility and are less well drained than soils derived from greywacke. (1) *G. montana* var. *stolonifera* has differentiated from *G. montana* on the granite ranges of North Westland. These granite ranges are separated to some degree from the Southern Alps. (2) *G. spenceri* and *G. tenuifolia* are western and eastern South Island species respectively. *G. spenceri* occurs mostly on granite mountains. Speciation may have been caused by a difference in rainfall, different forest types, or by the different rock type, or all three factors.

G. patula may have arisen by the isolation of a population of *G. montana*. The gap in the middle of its distribution in Nelson that is filled by *G. montana* could represent a later displacement by *G. montana* after *G. patula* speciated.

In a few cases, there is no obvious cause of speciation. The speciation of *G. cerina* and *G. concinna*, sympatric on the Auckland Islands, is the most puzzling case, as discussed above. *G. lineata* and *G. grisebachii* are sympatric in Fiordland and probably elsewhere. It is possible that *G. lineata* was isolated on Stewart Island from its *G. grisebachii* group ancestor, and that it subsequently dispersed back to Southland. *G. amabilis* and *G. bellidifolia* are sympatric in Otago and Southland. The two are separated by soil and soil moisture differences. From what is observable in the rest of the New Zealand species, it seems unlikely that this kind of difference in habitat would cause speciation without isolation.

In the foregoing discussion, it has been assumed that the distribution patterns have not been altered much by the cycles of glaciation. Burrows (1965) and Wardle (1988) hypothesised that both disjunctions in species distributions and vicariant species pairs between the north and south of the South Island were due to the effects of

glaciation in the central South Island. Burrows (1965) listed ten vicariance pairs and Wardle (1988) listed five vicariance pairs to support this hypothesis. Two of Burrows' pairs were gentians: *Gentiana lineata* of Otago-Southland-Stewart Island and *G. aff. lineata* of Nelson-Marlborough, and *G. montana* of Otago-Southland and *G. aff. montana* of Nelson-Marlborough. It is difficult to know what the two unnamed Nelson-Marlborough taxa represent, but no such vicariance pairs appear in my analysis. Burrows' *Raoulia rubra* and *R. buchananii* do not form a vicariance pair in the way suggested, nor do Wardle's *R. mammillaris* – *R. buchananii* pair (R. Smitsen, pers. comm.). *Dracophyllum densum* and *D. politum* do not form a vicariance pair as Burrows suggested nor do *D. menziesii* and *D. townsonii* (S. Venter, pers. comm.). Burrows' and Wardle's other pairs need confirmation. No disjunctions in distribution between northern and southern South Island gentian species are detectable, but in other genera these undoubtedly exist (e.g., in *Celmisia traversii*). Disjunctions due to glaciation are more plausible than vicariance pairs, because of the much shorter time scale needed to produce a geographical disjunction than a speciation event. Other disjunctions or vicariance pairs in the gentians may have been created by glaciers, but on a smaller scale than the whole South Island. For instance, the absence of *G. montana* on the Travers and St Arnaud ranges and its replacement there by *G. patula* may have a glacial explanation but this would be difficult to establish.

The age-area hypothesis

Willis's (1922) argument can be summarised as several points: (1) That neoendemics belong to non-endemic genera. They are abundant, and radiate into many species. (2) A distribution pattern showing concentric "wheels within wheels" is evident, and (3) The hub of the concentric wheels indicates the geographic centre of the radiation. (4) The age of species and the area they occupy are correlated. The oldest species form the outermost rims of the "wheels within wheels". (5) Outlying island floras will be older, as they will date to a time before sea barrier existed.

Which of these arguments are true for New Zealand *Gentianella*? The first argument is true of New Zealand *Gentianella*, and can be said to be true of some other New Zealand alpine genera that have radiated into many species, such as *Ranunculus*, *Myosotis*, *Epilobium*, and *Euphrasia*. On the other hand, there are alpine genera that have originated in New Zealand and had their main radiation here, and so are largely endemic. Examples are *Raoulia*, *Celmisia*, *Aciphylla*, and *Chionochoila*.

The second argument is untrue for New Zealand *Gentianella*. Speciation in

New Zealand *Gentianella* has largely been allopatric, if not always so. A concentric pattern of speciation cannot result from such a mode of speciation. The centre of diversity in New Zealand *Gentianella* is in Nelson, but this does not reflect the place of arrival of *Gentianella* in New Zealand, rather a second centre of radiation. In other alpine genera such as *Chionochloa* and *Aciphylla* the species seem evenly spread throughout the South Island.

The age of species of New Zealand *Gentianella* is, I believe, indicated to some degree by the extent of their distribution, in that the most widespread species, *G. montana* and *G. bellidifolia*, are in my opinion the oldest members of their respective groups. However, *G. saxosa* is not widespread but may be the oldest species of New Zealand *Gentianella*, and *G. lineata* is the most distinctive species of the *G. grisebachii* group and therefore may be the oldest species of that group but is not widespread. The converse is more likely to be true: that species with the smallest distributions are the youngest species. Examples are *G. filipes*, *G. luteoalba*, *G. magnifica*, *G. vernicosa*, *G. paparoaensis*, *G. angustifolia*, and *G. decumbens*.

Outlying island species of the *G. saxosa* group are likely to have diverged early in the New Zealand radiation, but *G. chathamica* appears to have a recent origin from a North Island *G. chathamica* population. Willis did not accept that dispersal across wide sea barriers occurs frequently. However, there is no support for New Zealand's outlying islands ever being connected to the main islands.

Gleason's (1924) more general statement of Willis's hypothesis, that distribution offers means of determining ancestry when used along-side phylogeny strikes me as true and represents a strand of thinking in botany that has been present since the time of J. D. Hooker's attempts to synthesise knowledge of distributions and classifications.

Relative proportions of sympatric and allopatric nearest-relations in New Zealand *Gentianella*

If every taxon recognised here as a species or subspecies is matched to its postulated nearest relative, the proportion of sympatric to allopatric taxa can be calculated. Of the 30 pairs of sibling taxa, 18 pairs of taxa are allopatric. Of these, eight pairs are species pairs (*G. divisa*/*G. luteoalba*, *G. divisa*/*G. filipes*, *G. divisa*/*G. magnifica*, *G. spenceri*/*G. chathamica*, *G. spenceri*/*G. tenuifolia*, *G. antarctica*/*G. antipoda*, *G. saxosa*/*G. cerina*, *G. saxosa*/*G. scopulorum*, and *G. concinna*/*G. antarctica*). Ten subspecies pairs are allopatric, six of these within *G. astonii* and *G. calcis*, two in *G. montana* and one in *G.*

chathamica. *G. montana* var. *stolonifera* and *G. montana* s. s. are allopatric in the South Island.

There are three pairs of taxa with distributions that overlap, but the members of the pairs are separated by altitude. Two of these pairs are species (*G. bellidifolia*/*G. serotina* and *G. gibbsii*/*G. grisebachii*) and one is a pair of subspecies, those of *G. corymbifera*.

There are seven sympatric pairs of species: *G. amabilis*/*G. bellidifolia*, *G. angustifolia*/*G. bellidifolia*, *G. corymbifera*/*G. divisa*, *G. impressinervia*/*G. montana*, *G. vernicosa*/*G. montana*, *G. bellidifolia*/*G. decumbens*, and *G. cerina*/*G. concinna*. One pair is only slightly overlapping: *G. montana*/*G. patula*. There is one species pair which meets along a boundary: *G. tenuifolia*/*G. stellata*.

Breeding systems and life-cycle

The breeding systems and pollination biology of the New Zealand gentians are an important part of understanding the genus here. In a few instances the most useful taxonomic characters are ones that reflect a selfing syndrome. Selfing is seen in reduced size of corolla and anthers, failure of the anthers to invert at the onset of the female phase of the flower, and failure of flowers to open. Female flowers are present on plants of some species, but is of limited taxonomic value because of its sporadic occurrence. Flower colour is a feature of the New Zealand gentians, and is most strongly expressed in the Subantarctic Islands where it appears to be polymorphic and associated with selfing. The cause of this polymorphism is still unexplained.

Frequent monocarpy is a special feature of *Gentianella*, with both annuals and biennials represented. The life cycle is usually constant within a species, in some cases separating groups of related species from others, and in other cases separating species from their closest relatives. In three well established cases, there is variation in life cycle within a species.

My conclusion is that the New Zealand gentian flora has only two truly annual species, *G. lilliputiana* and *G. filipes*. Both are small plants, and have very small taproots. I have no experience of the Subantarctic Island species in the field, but from Godley's (1982) observations, and my own observations of the size of individuals of *G. antipoda* in the herbarium, and the size of their taproots, I conclude that the three monocarpic gentians of the Subantarctic Islands are not true annuals, but are probably facultative biennials. The Subantarctic gentians are unusual among the New Zealand species in being lowland species and therefore not covered by snow during winter and

experience an oceanic climate with few extremes, and it is possible they may be able to germinate in late-summer, grow over winter and flower the following summer, concluding their lifecycle in 12 months. This could be tested in the field by tagging individual plants and following their development.

The phylogeny of the New Zealand species that I have attempted to reconstruct indicates that a change from polycarpic to monocarpic or the reverse happens infrequently, but at times quite easily. The *G. saxosa* group is the group of species with the most mixed life cycle, this being most obvious on the Auckland Islands where two sibling species are sympatric and *G. cerina* is polycarpic while *G. concinna* is monocarpic. *G. lineata* appears to have become polycarpic in a group of otherwise monocarpic species. *G. filipes* has become annual in a group of biennial species. *G. corymbifera* shows how easily the change from monocarpic to polycarpic can be made at times; a few populations of this species in Nelson and Westland are a mixture of biennial and polycarpic plants. The affinities of the annual species *G. lilliputiana* are too uncertain to draw any conclusions.

Table 3 indicates that the original state in *Gentianella* is monocarpy, with most species being facultative biennials, as this is the sole state found in Central Asia where the genus is hypothesised to have originated (Hagen & Kadereit, 2001). There has been a trend towards polycarpy in the Southern Hemisphere (South America and New Zealand). This trend has been reversed in Australia where most species appear to be facultative biennials.

Table 48 summarises the life cycle of the New Zealand gentians according to the authors who have written accounts of them. In the final column I have put my own estimate of the life cycle of the species. Godley (1982) cited Oliver & Sorensen (1951) as having noticed in January 1969 that *G. antarctica* showed three growth stages present at summer flowering time: young non-flowering plants, plants in flower or early fruit, and dying or recently dead plants. Godley surmises that *G. antarctica* has a life cycle of 18 months by germinating in spring, establishing a rosette during summer and overwintering in that state, followed by flowering and fruiting the following summer. This pattern is the same as that seen in biennial species of the New Zealand mainland. *G. antipoda* was thought to be perennial by Kirk, Cheeseman and Allan, but Godley notes that Cockayne (1904) suspected the species of being biennial, and cited Matthews' agreement on this from experience in cultivating the species. Godley (1982) notes that new flowering stems are produced from near the base of the primary stem. This is a characteristic of some polycarpic species on the New Zealand mainland, particularly in

the *G. montana* group. Godley concluded that both *G. antipoda* and *G. antarctica* are biennial, and I have followed this opinion. There is no evidence that these Subantarctic Island species are annuals.

Table 48 Life cycle according to previous studies and the present study. In the last column, changes from earlier authors are indicated in bold type.

Species	Kirk (1896)	Cheeseman (1925)	Allan (1961)	this study
<i>G. amabilis</i>	-	-	perennial (?)	perennial
<i>G. angustifolia</i>	-	-	-	perennial
<i>G. antarctica</i>	annual	annual	annual	biennial
<i>G. antipoda</i>	perennial	perennial	perennial	biennial
<i>G. astonii</i>	-	perennial	perennial	perennial
<i>G. bellidifolia</i>	perennial	perennial	perennial	perennial
<i>G. calcis</i>	-	-	-	perennial
<i>G. cerina</i>	perennial	perennial	perennial	perennial
<i>G. chathamica</i>	-	annual	annual	biennial
<i>G. concinna</i>	perennial (imp.)	usually annual	annual	biennial
<i>G. corymbifera</i>	perennial	perennial but...	perennial	usu. strict biennial/ occ. perennial
<i>G. decumbens</i>	-	-	-	perennial
<i>G. divisa</i>	perennial	not stated	perennial	triennial
<i>G. filipes</i>	-	annual	annual	strict annual
<i>G. gibbsii</i>	-	annual/perennial	annual (?)	biennial
<i>G. grisebachii</i>		annual	annual	biennial
<i>G. impressinervia</i>	-	-	-	perennial
<i>G. lilliputiana</i>	-	-	-	annual
<i>G. lineata</i>	perennial	perennial	perennial	perennial
<i>G. luteoalba</i>	-	-	-	biennial
<i>G. magnifica</i>	perennial	not stated	not stated	biennial / triennial
<i>G. montana</i>	-	annual(<i>G. tereticaulis</i>)/ perennial (<i>G. montana</i> , <i>G. townsonii</i>)	perennial	biennial/ perennial

Species	Kirk (1896)	Cheeseman (1925)	Allan (1961)	this study
<i>G. patula</i>	perennial	usu. perennial	perennial	perennial
<i>G. saxosa</i>	perennial	perennial	perennial	perennial
<i>G. scopulorum</i>	-	-	-	perennial
<i>G. serotina</i>	-	annual/biennial	biennial (?)	perennial
<i>G. spenceri</i>	annual	annual	annual	strict biennial
<i>G. stellata</i>	-	-	-	biennial
<i>G. tenuifolia</i>	-	appar. annual	perennial	strict biennial
<i>G. vernicosa</i>	-	perennial	perennial	perennial

The annual habit appears to be recently evolved in the New Zealand species, being present in only two species on the New Zealand main islands, *Gentianella lilliputiana* and *G. filipes*. *G. lilliputiana*'s nearest relative may be *G. magellanica*. Herbarium specimens of *G. magellanica* have the appearance of being biennial. The nearest relative of *G. filipes* appears to be *G. divisa*, a biennial or triennial species.

Monocarpy may be the primitive state in *Gentianella* in Asia, but polycarpy appears to be primitive in the New Zealand species if the *G. saxosa* group of species are basal. It is a life cycle that suits New Zealand plants because of the equability of the New Zealand climate and its lack of sharp and predictable seasons, which removes climatic selection pressure for monocarpy. A trend towards polycarpy in the Southern Hemisphere is evident.

Flower colour

Corolla colour is most intense in the *G. saxosa* group with the exception of *G. saxosa* which has white flowers. *G. scopulorum* has purple veins. Coloured veins are found in the *G. spenceri* group with the exception of *G. stellata*. All North Island gentians have coloured corolla veins. The largest corollae (which occur in the *G. divisa*, *G. montana*, and *G. bellidifolia* groups) tend to be the least coloured.

Godley's (1982) studies of the breeding system and flower colour in the Subantarctic Island gentian species suggest that strong flower colour is accompanied by a selfing syndrome as seen in small floral parts, particularly small anthers and few ovules per ovary. *Gentianella saxosa* is the exception in the *G. saxosa* group of species, in having white flowers and large flower parts, the large flowers suggesting that it is an outcrossing species. Godley (1982) noticed the association of flower colour and selfing

syndrome, and noticed that some colour is common in other New Zealand gentian species, but that it is stronger in the Subantarctic Island species. Godley's study and that of Lloyd (1985) make it seem unlikely that strong flower colour serves to attract pollinators. However, any other explanation of flower colour (e.g., warming of flowers due to greater adsorption of sunlight) must take account of what Godley recorded in some detail, that the Subantarctic gentian species are polymorphic for flower colour. This polymorphism suggests that there is frequency-dependent selection for both flower colour and lack of flower colour. It is difficult to see how if corolla colour functioned to warm or protect tissues from ultraviolet radiation it could show frequency-dependent selection. The studies of Brown & Clegg (1984) and Fry & Rauscher (1997) on *Ipomoea purpurea* show how the benefits of selfing in uncoloured flowers may balance the benefits of pollinator success in coloured flower forms. A line of investigation that should be followed is to find out whether in the Subantarctic Island gentians, white-flowered morphs show any difference in selfing rate compared to coloured morphs.

Some degree of colour is common in the corollae of South American and Australian species. It appears that the genes for colour expression are universally present but not expressed in some New Zealand species groups. An intense yellow colour in *G. impressinervia* seems to be an extension to the whole corolla tube of what is normally a yellow coloration in the nectary gland that must function to make the nectary more visible to pollinators.

Ecology

Gentianella has radiated into 30 species over two million years in New Zealand. It has paralleled other herbaceous genera such as *Epilobium*, *Chionochloa*, *Celmisia*, and *Euphrasia* in its success in the recently uplifted New Zealand mountains. New Zealand *Gentianella* species occupy very similar habitats to species of *Gentianella* in other parts of the world: coastal rocky habitats, open forests and forest margins, peat soil habitats including flushes in grasslands on hillslopes, valley floors, and lake and tarn margins; rocky talus slopes, shallow soils over limestone, and short grasslands and cushionfields.

New Zealand's gentian habitats are closest to those of Australia. Most species are alpine, with only a few being coastal. Most species grow in peaty wet soils, but quite a few grow in well drained soils of moderate to low fertility. A few are associated with limestone or marble. *Gentianella* throughout the world has a preference for open or lightly wooded habitats, wet soils, and sometimes an association with limestone. It appears that there has been a trend in the evolution of the group from more fertile soils

in the Northern Hemisphere to a stronger preference for infertile peaty soils, particularly overlying granite bedrock, in Australasia.

Epilobium in New Zealand is similar in occupying a wide range of habitats but with a stronger lowland presence, in lowland wetlands, dry banks and roadsides, cliffs and crevices, and shingle river-beds, as well as alpine tussocklands, induced montane tussocklands, flushes in these tussocklands, alpine fellfield and scree, and limestone soils. The two main differences between *Epilobium* and *Gentianella* in New Zealand are that *Epilobium* has not utilized the nutrient poor peat soils in the New Zealand mountains in the way that *Gentianella* has, and that it has no species exclusively of open forest and scrub or forest margins. These are two habitat types that *Gentianella* has occupied in the Northern Hemisphere. *Epilobium* in New Zealand shows a trend from being a genus of tall erect herbs in to smaller, less erect herbs of stonier, and somewhat drier habitats in New Zealand. *Gentianella* in New Zealand has become a successful competitor in the tall tussocklands as well as in drier stonier habitats on mountains.

The influence of the vegetation-dominating genus *Chionochloa* in the alpine zone is evident on some New Zealand *Gentianella* species, particular in Nelson, and this must also be the case for other important alpine herbaceous genera such as *Celmisia*. A dated phylogeny of *Chionochloa* in New Zealand related to its historical biogeography would contribute much to the understanding of the evolutionary history of a number of herbaceous alpine genera.

Taxonomic practice

Use of infraspecific ranks

McDade (1995) studied taxonomic practice in monographs and revisions, and found that overall, the authors of the treatments recognised infraspecific taxa in 10% of species they revised. Hamilton & Reichard (1992) made a similar study and found a similar figure of 8%. In *Gentianella*, I have recognised subspecies in 18% of species. In Australian *Gentianella*, Adams (1995) recognised subspecies in 29% of species, and in North American *Gentianella s. l.*, Gillett (1957) recognised subspecies in 46% of species. These high percentages suggest that *Gentianella* presents particularly high levels of geographic variation that needs to be expressed at subspecies level.

Authors of New Zealand revisions have generally recognised infraspecific taxa in a higher proportions of species than those reported by McDade: 9% in *Epilobium* (Raven & Raven 1976), 14% in the alpine Ranunculi (Fisher 1965), 18% in *Gnaphalium* sect. *Euchiton* (Drury 1972), 29% in *Asplenium* Brownsey (1977), 29% in *Leptinella*

(Lloyd 1972), and 33% in *Chionocholea* (Connor 1991). On the other hand, Heenan (1995 and 1996) recognised none in *Carmichaelia*. These high percentages (19% average for these seven cases) suggest that New Zealand's vascular flora has high levels of geographic variation.

The usual reason that authors give for recognising no infraspecific taxa in their revisions is that their level of knowledge of the group is insufficient to justify such a depth of treatment. A recent example was the revision of *Utricularia* by Taylor (1989), who recognised 214 species world-wide, but made no subspecies, explicitly giving the reason above for this. Klackenberg (1985) recognised no subspecies in 65 species of *Exacum* (Gentianaceae) saying that either there was insufficient material to get a clear picture of variation to apply the rank, or that solutions adopting either species or nothing were found on investigating the distribution of characters. Nor did he recognise any varieties, saying "If allopatric they have been ignored as taxa or regarded as species after studying the degree of differentiation and the distribution of characters".

Analysis of variation and measurement

The analysis using the Monte Carlo method (Schreider 1966) was conducted to find out how many specimens are enough to ensure that 95% of the natural variation in a quantitative character is encompassed within the minimum and maximum derived from a certain number of specimens. It found that 28–35 specimens will, on average, be sufficient regardless of the variation in the character being measured (Fig. 2–3). However, the standard deviation in this mean of 28–35 is high, such that on 10% of occasions, minima and maxima taken from that number of specimens will give an error rate of 10% or more. In most species I have measured for this revision, I have been unable to measure these numbers of specimens. To some degree, this has been offset by selecting the largest and smallest flowering plants in the field to bring back for measurement.

It can be asked, how much do inclusive limits matter? In the case of descriptions, users will not reject a species on the basis of a mismatch on one or two characters, especially if the mismatch is slight. For keys, both dichotomous and interactive, it matters a great deal. If a key couplet uses non-overlapping ranges, either the gap between the ranges needs to be large, or the sample size the ranges are based on needs to be large. For this reason, special effort needs to be made after construction of a key to check the ranges of such characters. A common problem for key users is disagreement amongst clauses within a couplet, and this often is the result of inadequate

sampling. In interactive keys, quantitative characters have a much stronger role because a gap between ranges is not necessary for a quantitative character to work. For instance, if species A has a leaf length of 10–20 mm and species B has a leaf length of 15–25 mm, then the key will exclude B for leaf lengths of 10–14 mm and exclude A for leaf lengths of 21–25 mm. Because quantitative characters are so useful in interactive keys, they need to be very reliable.

Extending the limits of minimum and maximum values is an option, in that it reduces the probability of rejection of the correct species. At the same time the probability of a failure to reject an incorrect species will be higher. A balance needs to be struck between the probability of a false exclusion of a species against the lack of exclusion of incorrect identifications and the user being forced to score new characters with further risk of error, or there being no further differences that will distinguish similar species.

Expression of quantitative characters in keys and descriptions

It is common practice in taxonomy to give only the upper limit of a range, e.g., "–25 mm long" in keys and descriptions. In such a case the user must assume that the character can range from 0–25 mm, when this is unlikely to be true. Authors may feel that the lower limit is indeterminate because plant dimensions increase up to a certain point, e.g., tree height increases steadily with age, up to a certain point. In most instances, a solution to this is that the dimensions should encompass all variation in adult plants, that is, ones that are reproducing.

Measurement accuracy is often expressed inconsistently, e.g., "2–2.5 mm" (Adams 1996). Such measurements should be given as "2.0–2.5 mm", as the last figure of a number gives the reader an approximate idea of the accuracy of a measurement. Unfortunately, many computer programs drop the "0" in these situations, even when the zero has been typed in, e.g., Lucid, Delta, and Systat, and the "0" has to be inserted to the text output from these programs.

A common fault in keys and descriptions is a failure to specify the dimension adequately, e.g., "pedicels 1–2 cm" (Adams 1995, p. 952, description of *Chionogentias diemensis*) and "anthers mostly 1.5–1.8 mm" (loc. cit, p. 950 couplet 2, "seeds 0.8–1 mm" (loc. cit. p. 951 couplet 4) without specifying that length or diameter is the dimension referred to.

Methods in quantitative taxonomy

Late in the first field season of this study, I chose to use Delta exclusively for coding and recording data because of the number of species involved. I found that the use of Delta had benefits beyond its function of producing standardised descriptions. The interactive key facility, Intkey, was valuable for showing which characters were most discriminating in the genus. The use of Intkey to identify new specimens gave immediate feedback on whether enough specimens had been sampled to encompass the variation within a species. When the interactive key works for most new specimens, the character states and ranges will be adequate if used in a dichotomous key. Delta also forces the taxonomist to define multi-state characters clearly, and shows up unsatisfactory coding.

The weakness of Delta is that the database is species-based, not specimen-based. Delta was not designed to be used at the stage where the classification is still fluid and specimens are sometimes being redetermined. A specimen-based data recording system is required for this. In Delta it is difficult to change existing characters or insert new ones, as the stack of existing data sheets no longer correspond to the new character set. For this reason, it is well worth finalising the character set before setting up the Delta files.

Comparison of means

I relied heavily on this analysis method in the revision because quantitative characters were often the best ones available in the absence of consistent qualitative differences. Principal components analysis also made the most of quantitative characters, and fortunately, the characters available had very varied eigenvectors. The use of wild material for both types of analysis limited their discrimination because of the effect of variation within a population. My solution to this was to supplement these objective analyses with a more intuitive approach, using my own impressions in the field and herbarium, and an understanding of geographic variation. Objectivity in taxonomic decision is desirable, but in practice it appears almost impossible to achieve.

Objectivity and subjectivity in taxonomic revisions

What is the place of quantitative analysis in taxonomic decision-making? Can the subjective and intuitive element be reduced, and if so, will better classifications result? At genus level and above, I believe so, if well supported analyses of whatever kind are used, for the reason that presenting an explicit analysis allows others to assess the

evidence for a taxonomic decision. At species level and below, I am less convinced. In this study a thoroughly and consistently objective analysis method leading directly to the classification was impossible to implement. Sometimes I made a taxonomic decision against the result of an analysis out of disbelief in the result. In doing this I am implicitly claiming that an intuitive approach can at times result in a better classification. While objectivity is a goal worth pursuing, and the results of objective analysis should be presented, authors must be convinced of the correctness of their results before basing a classification on these. The alternative that may be preferable in some cases, is to refrain from altering the existing classification where relationships are not well understood.

Examination of genus and species concepts have convinced me that there are two elements in these concepts. One is objective and is the monophyly criterion. This criterion can be simply stated, relates directly to our views on evolution, and can often be assessed with confidence. The other element, the level of difference that justifies recognition of a genus or species follows some approximate conventions that defy exact formulation that would ensure uniformity in biological classification. Formulations invoke numbers of differences, or size of gaps between groups of taxa, and they generally take into account the number of taxa involved. Where authors of revisions rely on the morphological-geographical species concept of Heywood (1963), there is no uniform view as to a minimum level of difference that justifies recognition of a species. In *Gentianella* and related genera, Gillett (1957), Adams (1995), and myself regarded six differences as sufficient for recognition of a species, while in the Compositae, Lowrey (1986) considered three differences to be sufficient.

Revisions that attempt to describe relationships between the taxa in a genus in some way (through tree diagrams derived by some means, or hierarchical groupings) provide a kind of interpretation of a genus that is sometimes omitted (e.g., by Raven & Raven 1976). When these relationships are presented, they can be combined with information about geographic distribution to make hypotheses about modes of speciation and areas of origin and radiation.

Taxonomic conclusions

This revision provides a new classification of the New Zealand gentians. It attempts to provide a classification that is comparable with revisions of *Gentianella* done in other countries and reflects hypothesised relationships within the New Zealand species. The pre-existing classification of the New Zealand gentians (that of Allan 1961) was

modified in several ways. Seven new species were recognised. Within five of the existing species, new subspecies were made to deal with strong geographic or altitude-based variation in situations where they could be delimited reasonably clearly. Other geographic variation was noted, particularly in *G. corymbifera*, *G. montana*, *G. grisebachii*, and *G. bellidifolia*, but not given taxonomic recognition. Two new synonyms (*G. gracilifolia*, *G. townsonii*) were made on the grounds that pairs of names described the same species. One synonym (*G. matthewsii*) was made on the grounds that the two named species intergraded in a way that could not be expressed in the classification. Of the varieties in the New Zealand gentians recognised by Allan (*G. montana* var. *stolonifera*, *G. divisa* var. *magnifica*, and *G. cerina* var. *suberecta*) two are recognised here: *G. divisa* var. *magnifica*, but as a species, and *G. montana* var. *stolonifera*.

At the start of the study, and in the course of field work, I considered a list of 24 candidate taxa, 12 of these proposed by A. P. Druce. The outcome of examination of these is that they were a mixture of new species (7 species), new subspecies (8 subspecies), variants that when seen in the larger context of the species they belonged within did not warrant recognition (7), of no perceivable difference from existing species (1), and based on a different chromosome count that could not be confirmed as a distinct entity (1). An important part of their assessment was to assign them correctly to a species group and to assess their distinctness relative to their most closely related species, or to find what species they belonged within.

Morphological evidence was sufficient to establish eight groups of species within New Zealand *Gentianella*. However, the deeper relationships between these groups are difficult to discern. This is likely to be the result of rapid diversification of the genus in New Zealand at an early stage in its radiation. This difficulty is likely to be reflected in the results of any future molecular studies. Nevertheless, it would be valuable to confirm the species groups described here by using a more variable region of the genome or by multiple-locus genetic fingerprinting.

Gentianella has been a difficult genus to revise in New Zealand and other parts of the world for two reasons. The first is that it has only recently radiated in the Southern Hemisphere. The second is that it has a paucity of qualitative characters, and attempts to find new taxonomically useful characters in leaf anatomy, leaf cuticles, pollen surface patterns, and seeds were largely unsuccessful. For this reason, I have relied heavily on statistical analysis of variation in quantitative characters. For this analysis, plants raised under uniform conditions would have been ideal, but raising large

numbers of plants in cultivation would have been extremely difficult. Therefore, wild populations have been used for the analyses. Principal components analysis and comparisons of means using the t-test present objectively the distinctness or lack of it between taxa for the characters chosen for these analyses and are useful in conjunction with information on geography and inferences as to the evolutionary history of species or subspecies. I have not always followed the results of these analyses where field observations indicated that taxa were more distinct than the analyses indicated.

When compared to other genera of flowering plants that have been revised in New Zealand, *Gentianella* has average amounts of infraspecific variation, as measured by the proportion of species with subspecies (18%), compared to other New Zealand flowering plant revisions (e.g., Lloyd 1972). Geographic variation within species often made it difficult to devise a workable classification, but this variation may be no more than that seen in other herbaceous genera that have radiated in the New Zealand mountains.

TAXONOMY

Gentianella Moensch, *Methodus Pl.* 482 (Moensch 1794) nom. cons. (S. Raucher 1976). Type: *Gentianella tetrandra* Moensch, loc. cit. nom. illeg., = *Gentianella campestris* (L.) Börner (fide Adams 1995).

= *Chionogentias* L.G.Adams, *Austral. Syst. Bot.* 8: 949 (1995). Type: *Chionogentias saxosa* (G. Forst.) L.G.Adams ibidem. Basionym: *Gentiana saxosa* G. Forst., *Kongl. Vetensk. Acad. Handl.* 38: 184, t.5 (1777).

Plants monocarpic and annual or biennial, or polycarpic and flowering each year; herbaceous (occasionally semi-woody). Leaves and stems glabrous. Caudex short and not distinct (less than 10 mm) to long and distinct (c. 150 mm), branched or unbranched; dead leaves caducous and leaving scars, or persistent and forming a shaggy layer on the caudex; new branches sometimes arising from old parts of the caudex. Leaves usually in rosettes, occasionally a rosette lacking in biennial plants in their second year, rosette either at the base of the terminal stem (in most monocarpic species) or at the apex of each branch (in most mature polycarpic species), opposite, decussate, sessile to petiolate, entire, elliptic, narrowly elliptic or linear, channelled to flat. Flowering stems single or multiple, either terminal from the rosette apex, or lateral from leaf axils below the rosette apex, erect to decumbent; with 1–6 pairs of opposite leaves that grade to being sessile in the upper parts of the stem, with four vertical ribs. Flowers scentless, protandrous, (4–)5(–6)-merous, on short to long pedicels that are square in section, terminal and solitary or terminal and lateral in dichasial cymes arising from scape leaf axils, 1–2 per axil. Calyx campanulate, lobed $\times 0.6$ – 0.85 , lobes slightly to strongly unequal in length and width, slightly V-shaped in section, usually erect, occasionally recurved, triangular to subulate, lobe margins smooth or papillose, apices acute (occasionally rounded), sinus narrowly to broadly acute, usually with a few hairs; the cup smooth or roughened, with hairs usually present on the inner surface, particularly at the calyx–corolla fusion line. Corolla campanulate, lobes overlapping in bud twisted anticlockwise, lobed $\times 0.65$ – 0.83 , lobes parting at anthesis to form a narrow-throated flower, or widely separating to form a stellar and salverform flower; corolla completely white, sometimes with tinting of grey-violet, pink, blue, dark purple or crimson in various parts of the corolla but usually at the apices on the outside surface, corolla rarely coloured uniformly, then pale yellow, veins colourless or crimson, purple, dark purple, or grey-violet; corolla tube white, green, or occasionally yellow; lobe sinuses a narrow

slit, hairs usually present on the inner corolla surface between the sinus and line of fusion of the filament to the corolla and as a ring just above the fusion line. Nectaries 0.4–1.5 mm from corolla base, alternate to and between the filaments, yellow to green, V- or U-shaped, bulbous or forming a pocket with a variably developed flap or two flaps, the flap when well developed sometimes with a toothed margin. Stamens alternating with the corolla lobes, medifixed, filaments flattened, pale translucent green. Anthers versatile, introrse before dehiscence, usually extrorse at dehiscence, sometimes remaining introrse or becoming horizontal at dehiscence, bilocular, locules oblong, purple-black, yellow or orange, dehiscing on the long axis outer wall, the mouth with a yellow, orange or red border. Male sterility occasional, in the form of anthers reduced or absent. Pollen yellow, rarely black through staining by the anther wall, 35–45 μm diameter, tricolpate, surface pattern surface striate or striate-reticulate, rarely reticulate. Ovary fusiform, unilocular with two opposite suture lines the length of the ovary, colour yellow, sometimes tinted blue or purple after fertilisation, style absent; stigma shortly bivalved, arms c. 0.7 mm long, stigmatic surface with clear or blue to purple-tinted clavate cells. Ovules attached by a short stalk to the inner surface of the outer ovary wall, in 4 equal rows, (2–)10–60(–80) per ovary. Capsule septicidal at the mouth, dry, brown, and leathery when seeds are ripe. Seeds spherical, c. 1.0 mm diameter, pale to dark brown, smooth. Chromosome number $2n = 36$. (based only on New Zealand species).

Collection methods to help with identification

Single plants can be difficult to determine when taken out of the context of their population. It will help with identification to note in the field: (1) Whether there are dead flowering stems on some plants. If present, they establish that the species is polycarpic. It is helpful to choose plants for pressing that include dead flowering stems to demonstrate this. (2) If dead plants are common at a site, it establishes that the species is monocarpic. It is helpful to press dead plants to demonstrate this on a herbarium specimen. (3) Whether there are rosette plants commonly present. If abundant, it establishes that the species is monocarpic and biennial. (4) Whole plants should be collected to show the structure of the plant, particularly whether flowering stems are terminal or lateral. (5) Flowers should be in late bud or in male phase, as all measurements given here are for flowers in male phase.

The key and descriptions are based on the specimens cited, as fresh plants or rehydrated herbarium specimens. In scoring the character states I have been inclusive

rather than exclusive. For instance, if stem colour might be judged crimson or purple-black, I have scored it as both. For common and widespread species, the maxima and minima of linear measurements should cover almost all plants that will be keyed out, but for species or subspecies that are rare, maxima and minima will underestimate natural variation.

Flowers on herbarium specimens can be rehydrated in hot water and measurements taken from them. It can be difficult to ascertain the stage of development of pressed flowers and those just opened should be selected.

Designation of types

ICBN article 9A.4 has been used as the basis for choosing the material designated as lectotype in some cases. The article states that "When a single collection is cited in the protologue but a particular institution housing this is not cited, it should be assumed that the specimen housed in the institution where the author is known to have worked is the holotype ..." (Greuter et al. 2000). Thus, the types of Petrie's and Kirk's species are at WELT, while those of Cheeseman are at AK and those of Hooker at K. In the case of Kirk's types, it is clear from annotations in Kirk's handwriting on the WELT specimens, sometimes in red ink, that these are types. At AK, Lucy Cranwell made choices of single plants on the sometimes numerous sheets of Cheeseman's specimens, but did not publish these lectotypifications. I have chosen single plants as lectotypes in accordance with ICBN article 8.2 (Greuter et al. 2000) and in many cases these coincide with Cranwell's unpublished choices.

Measurement conventions

(1.0-)2.0-7.0(-13.0) mm is to be interpreted as: rarely as small as 1.0 mm, usual minimum 2.0 mm, usual maximum 7.0 mm, rarely as large as 13.0 mm. Where a range is given in the form (1.0-)2.0-4.2-7.0(-13.0) mm, the middle number (in this example 4.2) is the mean estimated from the specimens used for the principal components analysis, in most cases the same as those listed under "Specimens examined".

Measurements of floral dimensions and some smaller leaf dimensions were made with a dissecting microscope with an eyepiece scale accurate to ± 0.05 mm. Measurements up to 12 mm long have this accuracy, while those longer than 12 mm are usually only accurate to ± 0.5 mm.

Bioclimatic zones

These follow Wardle (1991), and the zones used are montane (dominated by *Nothofagus* forests up to the upper altitude limit of *Weinmannia racemosa* and *N. fusca*), subalpine (dominated by short forest of *N. menziesii* and *N. solandri* var. *cliffortioides*, or where these are absent, scrub composed mainly of the epacrid and daisy families and conifers). In accordance with common useage in New Zealand I have used the term "alpine" very broadly for all areas above the subalpine zone, including what Wardle terms penalpine (dominated by *Chionochloa* species and herbaceous genera such as *Celmisia*) and alpine (above the limits of continuous grasslands).

Locality name

"Turks Cap Range" is the unnamed ridge to the west of Mt Owen, whose highest point is 1568 m at NZMS 260 M28 678664. This informal name follows useage by A. P. Druce, and appears on his and others' specimen labels.

Synopsis of informal groups

The *G. saxosa* group (*G. antarctica*, *G. antipoda*, *G. cerina*, *G. concinna*, *G. saxosa*, *G. scopulorum*).

Perennial (*G. saxosa*, *G. scopulorum*, *G. cerina*) or monocarpic (*G. concinna*, *G. antarctica*, and *G. antipoda*). Flowering stems decumbent (*G. saxosa*, *G. scopulorum*, *G. cerina*) or erect (*G. antarctica*, *G. antipoda*). Rosette leaves distinct in erect species, not distinct from stem leaves in flowering plants of decumbent species. Leaves green or tinted crimson beneath (in *G. cerina* and *G. antipoda*), usually succulent, sometimes with a thickened and recurved margin. Pedicels usually short, ≤ 18 mm long except in *G. saxosa*). Flowers small, ≤ 14 mm long except in *G. saxosa*), corolla coloured purple, violet or blue on the veins or tinting the corolla lobes (but white in *G. saxosa*). Anthers often small, (≤ 1.7 mm long in *G. antipoda*, *G. antarctica*, *G. cerina*, and *G. concinna*). Calyx deeply lobed, lobes often widest near the apex and sometimes rounded at the apex (narrowly triangular in *G. antipoda*), lobe margins serrated (in *G. antipoda*, *G. antarctica*, and *G. concinna*). Corolla sinus hairs sometimes absent (in *G. antipoda* and *G. antarctica*). Epidermal cells rectangular, shape factor 0.5–0.6. Pollen surface striate. Rock outcrops and peat turflands from sea level to the Subantarctic Island hilltops at 600 m.

The *G. divisa* group (*G. corymbifera*, *G. divisa*, *G. filipes*, *G. luteoalba*, *G. magnifica*). Monocarpic and biennial, but annual in *G. filipes*. Taproot robust (except in *G. filipes*). Caudex unbranched, with a single rosette of leaves. Terminal flowering stem green, crimson or purple-black, stout (except in *G. filipes*), often not visible because of condensation of flowering stem and the dense flower corymb. Leaves green, tinted purple-black sometimes in *G. corymbifera*, elliptic or strap-shaped and large (≤ 65 mm long in *G. corymbifera*, *G. magnifica*), usually flat but often V-shaped or channelled in the petiole, petiole relatively wide. Flowers forming a dense terminal corymb (except in *G. filipes*), medium sized, opening for pollinators, corolla white or yellow, very rarely tinted with pink or purple. Calyx lobes broadly triangular, width-to-length ratio of (0.35–)0.5–2.0. Anthers medium to long, 1.9–3.2 mm long except in *G. filipes*. Females flowers are sometimes present in *G. divisa* and *G. filipes*, rarely in *G. corymbifera*. Species of alpine tussockland, montane valley grasslands, fellfields and screes.

The *G. montana* group (*G. impressinervia*, *G. montana*, *G. patula*, *G. vernicosa*). Perennial, occasionally biennial, usually tall, 70–1500 mm. Caudex often branching with leaf rosettes on each branch, branches elongating with age, dead leaves dropping and leaving stem scars, sometimes with "stolons", i.e., new branches sprouting from older parts of the caudex. Flowering stems crimson or purple-black, terminal on main stem, or arising at apices of leaf rosettes. Leaves thick-textured, glossy above, green or tinted crimson below, rhomboid (*G. montana*), elliptic or obovate (*G. montana*, *G. impressinervia*) or narrowly elliptic (*G. vernicosa*), on a petiole of medium width (1.5–3.5 mm wide). Flowers medium sized (large in *G. impressinervia*), opening for pollinators. Calyx lobes not pandurate. Calyx sinus hairs usually present. Corolla white or with veins purple or violet, corolla tube sometimes yellow (*G. impressinervia*) or green (*G. montana*). Epidermal leaf cells rectangular in *G. vernicosa* and some *G. montana* populations, otherwise zigzagged. Pollen surface striate to striate-reticulate. Species of alpine tussocklands, occasionally of valley floor grasslands.

The *G. spenceri* group (*G. chathamica*, *G. spenceri*, *G. stellata*, *G. tenuifolia*). Biennial, of medium height, erect. Caudex unbranched and short, with a single distinct leaf rosette. Stems crimson, green, rarely purple-black or bronze (in some *G. stellata*). Leaves medium sized, not V-shaped in section, crimson on lower surface (except in *G. stellata*), thin in texture and matt adaxially (except in *G. stellata*). Flowers small (except in *G. stellata*), on short pedicels (except in *G. stellata*), opening for pollinators. Late

flowers often arising from the base of the terminal stem, often smaller than those of main inflorescence. Calyx lobes sometimes pandurate, narrow. Corolla white with purple or crimson veins (uncoloured in *G. stellata* and sometimes *G. chathamica*). Stigma sometimes coloured. Pollen surface semi-reticulate. Species of subalpine scrub and forest, and scrub and forest margins, fernlands, often on peat soils.

The *G. grisebachii* group (*G. gibbsii*, *G. grisebachii*, *G. lineata*).

Biennial (*G. gibbsii*, *G. grisebachii*) or perennial (*G. lineata*). Caudex unbranched, short. Flowering plants lacking a distinct rosette of leaves due to loss of first-year rosette leaves and elongation of stem base. Terminal flowering stem erect, purple-black, bronze, or green; lateral flowering stems often decumbent or semi-erect, arising from near the plant base. Leaves often small, flat, thin in texture, matt, sometimes tinted purple-black. Flowers solitary or few per flowering stem, on long pedicels, the pedicels elongating in late female phase. Flowers often small and then not often opening for pollinators. Calyx lobes narrowly triangular (width-to-length ratio of 0.21–0.27), tapering evenly. Anthers small (usually <2.0 mm long). Ovule number medium to high, 25–70. Corolla white or tinted violet, or with violet veins. Species of damp to wet mesotrophic to oligotrophic soils, montane to subalpine.

The *G. bellidifolia* group (*G. amabilis*, *G. angustifolia*, *G. bellidifolia*, *G. decumbens*, *G. serotina*).

Perennial. Caudex elongating with age and often branching, dead leaves on larger species not falling from the stem, accumulating as a shaggy layer. Distinct rosettes of leaves on each branch. Flowering stems arising from leaf axils below the terminal leaf rosette apex, green or purple-black, decumbent to semi-erect. Leaves yellow-green and untinted, sometimes tinted purple-black on the margins and petiole or speckled on the lamina surface (in *G. serotina* and *G. amabilis*), moderately thick, glossy adaxially, almost always distinctly V-shaped in section or channelled, petiole distinct, relatively narrow. Calyx lobes usually wide (usually 3.0–4.5 mm wide), lobe margins smooth or serrate, calyx sinus hairs usually abundant. Corolla white (never tinted purple, with coloured veins only in North Island *G. bellidifolia*), large (14–23 mm), opening to pollinators. Anther filaments sometimes wide (in *G. bellidifolia* and *G. amabilis* c. 2.0 mm wide), anthers large (1.7–2.6–3.9 mm long). Ovule number high, 25–40–60. Species of mostly alpine habitats, both well drained and moist.

The *G. astonii* group (*G. astonii*, *G. calcis*).

Perennial, plants often bushy. Caudex short, much branching in older plants, dead leaves not usually persistent. Rosette leaves not distinct from flowering stem leaves. Flowering stems lateral only (but usually obscurely so), usually branching repeatedly, usually purple-black. Leaves usually green (tinted purple-black in *G. astonii* subsp. *arduana* and *G. calcis* subsp. *waipara*), linear to narrowly elliptic, margins serrate or smooth. Calyx margins serrate, occasionally smooth, calyx sinus hairs usually abundant. Corolla white with uncoloured veins (except in *G. calcis* ssp. *manahune*), sometimes tinted violet at the lobe apices, not large (9.4–19 mm long), margins sometimes finely serrate. Nectary well developed and unusually distant (2–4 mm) from the corolla base, often pocket-shaped, the pocket margins sometimes toothed. Anthers usually purple-black, occasionally yellow, not large, 1.1–1.8–2.2 mm long. Ovule number low, 11–25(–34) per ovary. Species of coastal or montane soft Tertiary limestone in low rainfall areas.

The *G. lilliputiana* group (*G. lilliputiana*).

Annual, plants small. Taproot small and thin. Caudex short, unbranching, dead leaves not persistent. Leaf rosette absent from flowering plants. Flowering stems terminal or terminal and lateral, yellow-green, sometimes tinted purple-black. Leaves small, 3–8(–13) mm long, linear to narrowly elliptic, margins entire. Calyx and corolla 4-merous, glabrous. Calyx lobes as long as wide, green tinted purple-black. Corolla white, veins uncoloured. Anthers small (0.4–0.7 mm long), purple-black. Ovule number low, 2–4(–13) per ovary. A species of alpine oligotrophic cushion bogs.

Key to the species by group

- 1 plants annual; <25 mm tall; ovules 2–4(–13) per ovary; calyx lobes 4 per flower; pollen grain surface reticulate *G. lilliputiana*
plants biennial or perennial, rarely annual; (16–)25–600 mm tall; ovules usually >20 per ovary; calyx lobes usually 5 per flower; pollen grain surface pattern striate to striate-reticulate 2
- 2 plants often succulent and coastal, never alpine; Subantarctic Islands, Southland, rarely Westland; leaf and calyx margins often slightly thickened and recurved; calyx lobes sometimes rounded at the apices; pedicels usually short (1–12 mm); hairs at

- corolla sinus usually absent; abaxial leaf epidermal cells non-zigzagged pollen grain surface pattern striate *G. saxosa* group
- plants not succulent and not usually coastal, usually alpine; throughout New Zealand; leaf and calyx margins never thickened or recurved; calyx lobes never rounded at the apices; pedicels short to long; hairs at corolla sinus usually present; abaxial leaf epidermal cells usually zigzagged; pollen grain surface pattern semi-reticulate 3
- 3 plants monocarpic, corolla white (rarely tinted pink); flowering stem often condensed so that the stem is not visible; calyx lobes usually triangular (width to length ratio usually 0.5–2.0); South Island only *G. divisa* group
- plants polycarpic, or if monocarpic, then corolla veins usually coloured; flowering stem always visible; calyx lobes often narrowly triangular (width-to-length ratio 0.2–0.8); North Island and South Island, Chatham Islands 4
- 4 flowering stems always arising from below the apex of leaf rosettes; plants polycarpic; corolla usually white 5
- flowering stems arising at the leaf rosette apex; plants usually monocarpic; corolla usually with coloured veins 6
- 5 leaves linear to narrowly elliptic; plants often bushy and much-branched, flowering stem leaves not different from leaves at the plant base; flowers small, corolla 9–15(–19) mm long; anthers 1.1–2.2 mm long; ovules 11–25(–34) per ovary; plants of coastal and montane Tertiary limestone outcrops in Marlborough, Canterbury, and Otago *G. astonii* group
- leaves narrowly elliptic to orbicular; plants not bushy, sparsely branched, flowering stem leaves sessile and smaller than rosette leaves; flowers large, corolla 14–25 mm long; anthers 1.7–3.9 mm long; ovules 25–60 per plant; plants usually alpine *G. bellidifolia* group
- 6 caudex (10–)15–120(–300) mm long and branching, with scars from fallen leaves *G. montana* group
- caudex 7–30(–100) mm long and unbranched, or if branched, then plants small (<100 mm tall); caudex without obvious leaf scars 7

- 7 pedicels not elongating markedly after flowering, short (1–20 mm long) in most species but up to 45 mm in others; rosette of leaves persisting in flowering plants *G. spenceri* group
- pedicels elongating markedly after flowering, always long (10–80 mm long); rosette of leaves not usually persisting in flowering plants *G. grisebachii* group

***G. saxosa* group**

- 1 plants polycarpic; branches and flowering stems decumbent 2
- plants monocarpic; terminal flowering stem erect 3
- 2 leaf petiole 11–13 mm long; calyx 9.3–12.2 mm long; corolla small (8.4–11.8 mm long), varying between white and dark red, nectaries only 1.2–1.5 mm from the base of the corolla; Auckland Islands *G. cerina*
- leaf petiole 14.5–64 mm long; calyx 7.2–8.8 mm long; corolla large (13.7–15.8 mm long), usually uniformly white, nectaries 2.5–3.7 mm from the base of the corolla; Southland, Stewart Island 3
- 3 corolla veins colourless; leaves elliptic to narrowly elliptic; calyx lobes recurved; flowering stems purple-black; anthers 2.0–2.1 mm long; Southland, Otago *G. saxosa*
- corolla veins purple; leaves orbicular; calyx lobes plane; flowering stems crimson; anthers 1.0–1.5 mm long; Westland *G. scopulorum*
- 4 hairs at corolla sinus present; leaf apex rounded; pedicels 4.0–7.0(–11.5) mm long; calyx lobes 2.0–2.3 mm long; Auckland Islands *G. concinna*
- hairs at corolla sinus absent; leaf apex acute to rounded; pedicels 0.8–4.5 mm long and not easily seen; calyx lobes 3.9–6.7 mm long; Campbell Island and Antipodes Island 5
- 5 plants usually with only a central flowering stem, occasionally up to 4 lateral flowering stems; rosette leaf petiole 1.6–2.6 mm long; corolla tube 3.6–4.4 mm long; nectaries 1.6–3.4 mm from corolla base; ovules many, (7–)8–23(–27) per ovary; capsule 8.0–13.2 mm long; Campbell Island *G. antarctica*
- plants with 2–20 lateral flowering stems; rosette leaf petiole 3.2–3.5 mm long;

corolla tube 1.6–2.9 mm long; nectaries 1.0–1.4 mm from corolla base; ovules few, (3–)4–7(–9) per ovary; capsule 2.9–7.2 mm long; Antipodes Islands . *G. antipoda*

G. divisa group

- 1 plants annual, taproot slender, <1.0 mm diameter; flowers 1–14(–81) per plant, corolla 7.6–12.0 mm long; calyx lobes wider than long *G. filipes*
plants biennial or triennial, taproot thick >1.0 mm diameter; flowers 11–250 per plant, corolla 11.0–22 mm long; calyx lobes longer than wide 2
- 2 flowering stem not condensed, main stem easily visible and distinguishable from any lateral flowering stems; plants tall, (90–)160–470 mm high *G. corymbifera*
flowering stem condensed so that the main stem is not usually visible; plants small, 25–200 mm high 3
- 3 plants small, 25–60 mm high; corolla pale yellow; filaments 0.6–0.8 mm wide; abaxial epidermal leaf cells non-zigzagged with thickened walls *G. luteoalba*
plants large, (40–)60–150(–200) mm high; corolla white; filaments 0.9–2.9 mm wide; abaxial epidermal leaf cells zigzagged with thin walls 4
- 4 leaves (35–)51–105 mm long; root stout, 8–13 mm diameter; calyx 12.3–20 mm long; corolla 17.2–24.5 mm long *G. magnifica*
leaves 16–65 mm long; root more slender, 2.0–6.0 mm diameter; calyx 8.5–11.0 mm long; corolla 13.5–18.6 mm long *G. divisa*

G. astonii group

- 1 leaves 9–32 mm long, plane, apex not recurved *G. astonii*
leaves 30–83 mm long, usually folded, apex recurved *G. calcis*

G. bellidifolia group

- 1 leaf petioles 4.1–6.9 mm wide, leaves 40–120 mm long and 10–16 mm wide; Nelson, on marble rock outcrops and related shallow soils *G. angustifolia*
leaf petioles usually <4.0 mm wide, leaves (10–)20–44(–160) mm long and

- (3.5-)4.0-10(-25) mm wide; North Island and South Island, not associated with limestone 2
- 2 leaves purple-speckled, (10-)20-46(-52) mm long; flowers usually 1 per flowering stem; flowering stems 1-3(-8) per plant; calyx lobes 3.1-4.7 mm wide
..... *G. amabilis*
leaves green, or if purple-speckled then >50 mm long; flowers usually more than 1 per flowering stem; flowering stems 1-13 per plant; calyx lobes 1.4-3.6 mm wide
..... 3
- 3 leaves (32-)45-112(-160) mm long, very narrow elliptic (length-to-width ratio rarely less than 6:1), not channelled, sometimes slightly V-shaped in section; calyx lobes (2.1-)2.3-2.6(-3.0) mm wide; plants usually >140 mm high *G. serotina*
leaves (11-)20-44(-142) mm long, orbicular to narrowly elliptic (length-to-width ratio usually <6:1), channelled except when >80 mm long; calyx lobes (2.0-)2.5-2.9(-3.5) mm wide; plants usually <140 mm high 4
- 4 plants 170-400 mm diameter with long prostrate branches, circular in outline with flowers on the perimeter; flowering stems many, (1-)4-12-22(-27) per plant, green without secondary pigments; leaves (16-)20-44(-48) mm long; calyx lobes (2.3-)2.9-3.9(-5.1) mm wide; nectary (1.0-)1.6-2.3 mm from corolla base; Nelson, alpine, usually on summit fellfields *G. decumbens*
plants smaller, rosettes without prostrate spreading branches, flowers on decumbent branches; flowering stems fewer, 1-6(-11) per plant, green or tinted purple-black, leaves 11-52-100(-140) mm long; calyx lobes (1.7-)2.0-3.6(-6.0) mm wide; nectary 0.4-1.1(-1.4) mm from corolla base; North Island and South Island in moist to well drained habitat, occasionally on summit fellfields
..... *G. bellidifolia*

G. montana group

- 1 corolla tube yellow; 3 impressed veins visible on upper leaf surface; stolons usually present; filaments 1.5-1.7 mm wide; anthers 2.8-3.9 mm long; Glasgow Range to Crawford Range *G. impressinervia*
corolla tube white or green, the midvein only visible on upper leaf surface; stolons

- sometimes present; filaments 0.6–1.5(–1.8) mm wide; anthers 1.7–2.9(–3.0) mm long; North Island and South Island 2
- 2 leaves 1.8–5.7(–6.0) mm wide without a distinct petiole, leaves thick (0.67–0.78 mm thick); plants 80–190 mm tall; Westhaven Inlet to Matiri Plateau *G. vernicosa*
leaves (3.5–)5.4–18 mm wide, usually with a distinct petiole, leaves thin (0.26–0.46 mm thick); plants (130–)170–370 mm tall; North and South Islands 3
- 3 calyx lobes 5.3–9.6 mm long; caudex unbranched to sparsely branched; flowers per plant few, 4–48; leaves (5.5–)7.0–18 mm wide *G. montana*
calyx lobes 3.4–6.0 mm long; caudex much branched with many flowering stems; flowers per plant many, 40–126; leaves (3.5–)5.0–9.0 mm wide *G. patula*

G. spenceri group

- 1 corolla veins uncoloured; anthers yellow; leaves channelled; flowering stem leaves and calyx lobes strongly recurved; on ultramafic soils in Nelson *G. stellata*
corolla with purple veins; anthers blue-black; leaves not channelled; flowering stem leaves and calyx lobes not recurved; never on ultramafic soils 2
- 2 plants 210–530 mm tall; rosette leaves narrowly elliptic, 68–102 mm long, leaf petiole not very distinct; flowering stem leaves 4–6 pairs per stem; pedicels long, 6–24 mm long; Nelson, Marlborough, Canterbury, Westland *G. tenuifolia*
plants 60–190 mm tall; rosette leaves orbicular to ovate, 18–75 mm long, leaf petiole distinct; flowering stem leaves 1–2 pairs per stem; pedicels short, 1–10(–20) mm long 3
- 3 leaves 25–80(–93) mm long, 13–22 mm wide; calyx lobes 5.7–9.3 mm long; pedicels 1–10 mm long; Nelson, Westland *G. spenceri*
leaves 18–31(–43) mm long, 6–10 mm wide; calyx lobes 3.0–6.1 mm long; pedicels 4–20 mm long; North Island, Chatham Islands *G. chathamica*

G. grisebachii group

- 1 plants small, (30–)70–100(–180) mm tall; flowers solitary on each flowering stem,

- flowering stem leaves absent or one pair per stem; pedicels 0.5–0.8 mm diameter
 *G. lineata*
- plants large, (70–)120–600 mm tall; flowers usually more than 1 per flowering stem,
 flowering stems leaves 3–4 pairs per stem; pedicels 0.5–1.4 mm diameter 2
- 2 calyx lobes 8.5–12 mm long; rosette of leaves persisting on flowering plants; Stewart
 Island *G. gibbsii*
- calyx lobes 4.2–7.8 mm long; rosette of leaves not persisting on flowering plants;
 Stewart Island to Hikurangi *G. grisebachii*

Key to the species by island

Separate keys for each island in New Zealand reduces the difficulty of each key. Three island groups have a single species. For the remainder, a key to each island is provided.

CHATHAM ISLANDS: *G. chathamica* subsp. *chathamica*

ANTIPODES ISLANDS: *G. antipoda*

CAMPBELL ISLAND: *G. antarctica*

NORTH ISLAND

- 1 flowering plants never with terminal flowering stems present, flowering stems lateral
 only; perennial *G. bellidifolia*
- flowering plants always with terminal flowering stems present; biennial 2
- 2 pedicels 3–9(–17) mm long; anthers 0.4–1.1 mm long
 *G. chathamica* subsp. *nemorosa*
- pedicels (10–)13–80 mm long; anthers (0.8–)1.0–3.0 mm long 3
- 3 plants often with only a single, terminal flowering stem; lateral flowering stems
 when present also erect; pedicels 8–35 mm long *G. montana* subsp. *ionostigma*
- plants always with lateral flowering stems present, lateral flowering stems
 decumbent; pedicels (10–)13–65 mm long *G. grisebachii*

SOUTH ISLAND

- 1 plants with leaves <3.0 mm wide 2
- plants with leaves >3.0 mm wide 3

- 2 plants on coastal and montane limestone, flowering stem leaves present, not distinguished from basal leaves *G. astonii*
- plants in coastal to alpine moist peat soils, flowering stem leaves absent .. *G. lineata*

- 3 plants strictly coastal, on sand or rock outcrops, succulent from salt influence 3
- plants mostly alpine, never coastal 4

- 4 corolla veins colourless; leaves elliptic or narrowly elliptic; calyx lobes recurved; flowering stems purple-black; anthers 2.0–2.1 mm long *G. saxosa*
- corolla veins purple; leaves orbicular; calyx lobes plane; flowering stems crimson; anthers 1.0–1.6 mm long *G. scopulorum*

- 5 flowering plants with lateral flowering stems only, always perennial; caudex when long shaggy with dead leaf bases; leaves usually channelled (U-shaped in section) 6
- flowering plants always with a terminal flowering stem; perennial or monocarpic; if caudex is branched, then rosettes have terminal flowering stems; caudex when long not shaggy with dead leaf bases; leaves flat or V-shaped in section 12

- 6 leaves linear to narrowly elliptic; plants often bushy and much branched, flowering stem leaves not different from leaves at the plant base; flowers small, corolla 9–15(–19) mm long; anthers 1.1–2.2 mm long; ovules 11–25(–34) per ovary; plants of coastal and montane Tertiary limestone outcrops in Marlborough, Canterbury, and Otago 7
- leaves narrowly elliptic to orbicular; plants not bushy, sparsely branched, flowering stem leaves sessile and smaller than rosette leaves; flowers large, corolla 14–25 mm long; anthers 1.7–3.9 mm long; ovules 25–60 per plant; plants usually alpine 8

- 7 leaves 9–32 mm long, plane, apex not recurved *G. astonii*
- leaves 30–83 mm long, usually folded, apex recurved *G. calcis*

- 8 leaf petioles 4.1–6.9 mm wide; Nelson, on marble rock outcrops and associated shallow soils *G. angustifolia*
 leaf petioles <4.0 mm wide; North Island, South Island, not on marble 9
- 9 leaves purple-speckled, leaves 20–46(–52) mm long; flowers usually 1 per flowering stem; flowering stems 1–3(–8) per plant; calyx lobes 3.1–4.7 mm wide
 *G. amabilis*
 leaves green, or if purple-speckled then leaves >50 mm long; flowers usually more than 1 per flowering stem; flowering stems 1–13 per plant; calyx lobes 1.4–3.6 mm wide 10
- 10 leaves (32–)45–112(–160) mm long, very narrow elliptic (length-to-width ratio rarely <6:1), not channelled, sometimes slightly V-shaped in section; calyx lobes (2.1–)2.3–2.6(–2.9) mm wide; plants usually >140 mm high *G. serotina*
 leaves (11–)20–44(–142) mm long, orbicular to narrowly elliptic (length-to-width ratio usually <6:1), channelled except when >80 mm long; calyx lobes (2.0–)2.5–2.9(–3.5) mm wide; plants usually <140 mm high 11
- 11 plants 170–400 mm diameter with long prostrate branches, circular in outline with flowers on the perimeter; flowering stems many, (1–)4–12–22(–27) per plant, green without secondary pigments; leaves (16–)20–44(–48) mm long; calyx lobes (2.3–)2.9–3.9(–5.1) mm wide; nectary (1.0–)1.6–2.3 mm from corolla base; Nelson, alpine, usually on summit fellfields *G. decumbens*
 plants with erect branches; flowering stems few, 1–6(–11) per plant, green or tinted purple-black, leaves 11–52–100(–140) mm long; calyx lobes (1.7–)2.0–3.6(–6.0) mm wide; nectary 0.4–1.1(–1.4) mm from corolla base; North Island, South Island
 *G. bellidifolia*
- 12 stolons present; leaf scars visible on caudex 13
 stolons absent; leaf scars not visible on caudex 15
- 13 corolla tube yellow; leaves with lateral veins often impressed in upper leaf surface .
 *G. impressinervia*
 corolla tube white or green; lateral veins never impressed in upper leaf surface .. 14

- 14 leaves without a petiole, narrow, (1.8–)2.4–5.7(–6.0) mm wide; leaves thick in texture (0.67–0.78 mm thick) *G. vernicosa*
leaves with a distinct petiole, (3.5–)9.5–18 mm wide; leaves not thick in texture (c. 0.25–0.45 mm thick) *G. montana*
- 15 corolla white with veins coloured crimson, purple or blue 16
corolla white or yellow with veins not coloured 19
- 16 calyx lobes pandurate; pedicels short (1.5–10 mm long) *G. spenceri*
calyx lobes not pandurate; pedicels usually longer than 10 mm 17
- 17 rosettes more than 1 per plant, caudex branched 18
rosettes 1 per plant, caudex unbranched 19
- 18 calyx lobes 5.3–9.6 mm long; caudex unbranched to sparsely branched; flowers per plant few, 4–48; leaves (5.5–)7.0–18 mm wide *G. montana*
calyx lobes 3.4–6.0 mm long; caudex much branched with many flowering stems; flowers per plant many, 40–126; leaves (3.5–)5.0–9.0 mm wide *G. patula*
- 19 plants 40–290 mm tall; leaf petiole 11–16 mm long, 0.7–2.3(–3.6) mm wide; North Island, South Island, plants of open wetlands and moist grasslands, under forest in North Island only *G. grisebachii*
plants 230–530 mm tall; leaf petiole 30–33 mm long, 3.0–4.8 mm wide; Nelson, Canterbury and Westland; plants of forest and scrub *G. tenuifolia*
- 20 plants <30 mm in height 21
plants ≥30 mm in height 23
- 21 corolla pale yellow, flowers many (14–133 per plant); biennial *G. luteoalba*
corolla white (occasionally tinted violet), flowers usually fewer than 14 per plant; annual 22
- 22 ovules >10 per ovary; anthers 0.8–1.4 mm long; Nelson, in well drained soils, talus and rock outcrops *G. filipes*
ovules c. 2–4(–13) per ovary; anthers 0.4–0.7 mm long; Otago, in wet peat soils of

cushion bogs	<i>G. lilliputiana</i>
23 plants biennial or annual; if biennial then flowers in dense corymbs	24
plants perennial, or if biennial then flowers not in dense corymbs	27
24 stems ≥ 4.0 mm diameter; leaf petiole ≥ 4.0 mm wide	25
stems < 4.0 mm diameter; leaf petiole < 4.0 mm wide	26
25 ovules 36–68 per ovary; plants (60–)160–470 mm tall	<i>G. corymbifera</i>
ovules 9–20 per ovary; plants 70–190 mm tall	<i>G. magnifica</i>
26 calyx lobes 5.0–9.0 mm long; anthers 1.9–2.8 mm long; biennial; Southland, Otago, Westland, Canterbury	<i>G. divisa</i>
calyx lobes 2.6–5.0 mm long; anthers 0.8–1.4 mm long; annual; Nelson ..	<i>G. filipes</i>
27 caudex never branched; biennial	28
caudex usually branched; biennial or perennial	29
28 leaves thin, not V-shaped in section; calyx lobes not recurved; widespread	
.....	<i>G. grisebachii</i>
leaves thick, V-shaped in section; calyx lobes recurved; Nelson, on ultramafic soils	<i>G. stellata</i>
29 leaves without a petiole, narrow, 2.4–5.0(–6.0) mm wide; leaves thick in texture ...	
.....	<i>G. vernicosa</i>
leaves with a distinct petiole, wide, (3.5–)9.5–18 mm wide; leaves not thick in texture	30
30 calyx lobes 4.1–4.5 mm long; caudex unbranched or sparsely branched	
.....	<i>G. montana</i>
calyx lobes 4.4–8.7 mm long; caudex much branched with many flowering stems ..	
.....	<i>G. patula</i>

STEWART ISLAND

- 1 calyx lobes narrowly triangular, apices narrowly acute; plants not succulent 2
calyx lobes not narrowly triangular, apices rounded-acute; plants succulent
. *G. saxosa*
- 2 caudex much branching; leaves narrow, <3 mm wide *G. lineata*
caudex unbranched; leaves wider, >3 mm wide 3
- 3 calyx lobes 8.5–12 mm long; Mt Anglem only *G. gibbsii*
calyx lobes 4–8.0 mm long; montane wetlands *G. grisebachii*

AUCKLAND ISLANDS

- 1 perennial; flowering stems all decumbent; calyx 9.3–12.2 mm long, calyx lobes
pandurate, rounded at the apices; corolla shorter than the calyx; leaves 36–53 mm
long, 8.4–12.6 mm wide *G. cerina*
biennial; terminal flowering stem erect; calyx 6.0–8.8 mm long, calyx lobes not
pandurate, rounded to acute at apices; corolla longer than the calyx; leaves 15–32
mm long, 3.7–8.0 mm wide *G. concinna*

DESCRIPTIONS

Gentianella amabilis (Petrie) Glenny, comb. nov.

Basionym: *Gentiana amabilis* Petrie, *Trans. & Proc. New Zealand Inst.* 56: 14 (1926).

Lectotype (here chosen): *W. A. Thomson*, "In bogs top of Mt Tennyson, Garvie Range Southland, 2:4:1921", WELT 4712a!

DESCRIPTION: Plants polycarpic, height in flower 30–80–130 mm. Caudex unbranched, c. 80 mm long. Root unbranched, 1.5–6.0 mm diameter at stem base. Flowering stems lateral only, 1–2–5 per plant, 1.1–2.0 mm diameter at base, stems tinted purple-black; lateral flowering stems erect or decumbent; flowering stem leaves 1–4 pairs per stem, lowest pedicels from near apex of flowering stem. Rosette of leaves distinct from flowering stem leaves; leaves narrowly elliptic or elliptic, (10–)20–30–46(–52) mm long, 3.5–9.2–12.0 mm wide, tinted crimson below or tinted purple-black and speckled

purple, channelled (petiole channelled also), not recurved, petiole indistinct to distinct, 9.5–12.5 mm long, 1.0–2.4–4.1 mm wide; apex acute or rounded. Flowering stem leaves as for rosette leaves but the upper ones sessile. Pedicels one per leaf axil, 3–37 mm long, 1.2–1.5 mm diameter. Flowers 1–3.4–8 per plant, 15–23 mm long. Calyx 7.5–10.3–14.2 mm long, green tinted purple-black, hairs at calyx-corolla fusion line absent or present; lobes 4.5–6.8–9.5 mm long, 3.1–3.7–4.7 mm wide at base, plane, apices acute, margins smooth or minutely serrulate, sinus hairs sparse. Corolla 11.8–18.4–22.5 mm long, white; tube 3.5–6.0 mm long; lobes 9.7–16 mm long, 5.8–10.6 mm wide, hairs below sinus absent or present; nectary 0.8–1.2–1.8 mm from corolla base. Filaments 7.5–13 mm long from corolla base, 0.9–1.7–2.0(–2.6) mm wide. Anthers 1.7–2.4–3.0 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis; pollen yellow. Stigma colourless. Ovules 28–40–56 per ovary. Capsule 20–27 mm long. FL. late Jan–late Feb.

DISTRIBUTION (Fig. 47): OTAGO: Dunstan, Hawkdun, Lammermoor Range, Old Man Range, Old Woman Range, Remarkables, Umbrella Mountains, Pisa Range.

SOUTHLAND: Garvie Mountains, Mavora, Mt Burns.

HABITAT: Alpine cushion bogs and low-angled flushes, with *Carex gaudichaudiana*, *C. echinata*, *Isolepis aucklandica*, *Agrostis subulata*, *Psychrophila obtusa*, *Polytrichum commune*, *Syntrichia robusta*, *Campyllum stellatum*, *Marchantia berteroana*, and *Sphagnum cristatum*; 975–1675 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980), $n = 18$ (Post 1983).

RECOGNITION: Most similar to *G. bellidifolia* in having channelled leaves, a long narrow petiole, large white flowers, decumbent, lateral flowering stems. It differs in being shorter, 30–50–130 mm tall (Otago *G. bellidifolia* is 70–140–280 mm tall); having purple-spotted leaves with a dark purple petiole (green and unspotted in *G. bellidifolia*), and fewer flowers, 1–2–5 per plant (Otago *G. bellidifolia* has 4–11–26 flowers per plant); and fewer flowering stems, 1–1.5–3 per plant (Otago *G. bellidifolia* has 1–3.0–4 stems per plant). The calyx lobes are wider, 3.1–4.0–4.7 mm wide (1.7–3.0–4.2(–4.4) mm wide in *G. bellidifolia*), and the filaments are wider, (0.9–)1.1–1.7–2.6 mm wide (0.6–1.2–1.4(–1.9) mm wide in *G. bellidifolia*).

VARIATION: Most plants seen are small compared to *G. bellidifolia*, but occasionally individuals match the size of Otago *G. bellidifolia*.

SPECIMENS EXAMINED: *D. Glenny* 6383, Garvies, CHR 509909; *D. Glenny* 6862, Remarkables, CHR 559424; *D. Glenny* 6887, Old Man Range, CHR 559448; *C. Jensen*, Lammermoor Range, CHR 526407.

CONSERVATION STATUS: Restricted in its range, but common in its habitat and not threatened.

ETYMOLOGY: *Amabilis* means "pleasing".

ILLUSTRATION: Johnson (1997, p. 115).

DISCUSSION: In cultivation, plants maintain the purple petiole and spotted leaves. Sympatric with *G. bellidifolia* in many places (e.g., at the southern end of the Old Man Range). On the type, Petrie singles out two plants for having two flowers each, while the remaining twelve plants have only one flower per plant. This indicates that Petrie considered the few flowers per plant to be a distinctive feature of the species.

Gentianella angustifolia Glenny, sp. nov.

DIAGNOSIS: *Gentianellae bellidifoliae* affinis, sed statura maiore, caudice magis ramoso, prostratis, longo, fasciculato (non radianti), ad basem foliis mortuis vestito, foliis maioribus, planis (nec carinatis nec canaliculatis), petiolo latiore 3.6–5.3–7.6, floribus maioribus (corolla 14.2–17.0–24.5(–27) mm longa), lobis calycinis ad basem latis: (2.6–) 3.1–4.0–5.6 mm, statione in fissuris petraeis marmoreis differt.

HOLOTYPE: A. P. Druce, "Turks Cap Range", NW Nelson, 1200 m, cliff (calcareous), M28 68-65-, Feb 1989, CHR 395647! Isotypes: CHR 395645 and 395646.

DESCRIPTION: Plants polycarpic, height in flower 110–220–300(–360) mm. Caudex branched (6–8 times), 45–150 mm long, covered in a brown shaggy layer of dead leaf bases, stolons absent. Root 2.4–8.5 mm diameter at stem base. Flowering stems lateral only, (1–)4–7–10 per plant, largest flowering stems 1.4–3.5 mm diameter at base, stems purple-black, decumbent, stem leaves 2–3 pairs per stem, lowest pedicels from halfway

up to near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves narrowly elliptic or elliptic, (23-)25-79-110(-161) mm long, (6.4-)10-13-16(-30) mm wide, green, sometimes tinted purple-black on the margins, flat; petiole absent or indistinct, leaf 3.6-5.3-7.6 mm wide at narrowest point, sometimes with a V-shaped petiole; apex acute or rounded. Pedicels one or two per leaf axil, 10-80 mm long, 1.0-1.8 mm diameter. Flowers (3-)10-27-43(-48) per plant, 18-25 mm long. Calyx (9-)12-14-18 mm long, green, sometimes tinted purple-black on margins, hairs at calyx-corolla fusion line present, rarely absent; lobes (5.6-)8.0-9.5-12.5 mm long, (2.6-)3.1-4.0-5.6 mm wide at base, plane, apices acute, margins smooth or minutely serrulate, sinus hairs sparse to abundant, with tips often purple. Corolla 14.2-17.0-24.5(-27) mm long, white; tube 3.9-5.8(-6.2) mm long; lobes 10.3-15.6 mm long, 6.4-13 mm wide, hairs below sinus present or absent; nectary (0.6-)0.9-1.1-1.4(-2.9) mm from corolla base. Filaments 7.9-12.3 mm long from corolla base, 0.8-1.2-1.4(-1.5) mm wide. Anthers 1.9-3.0-3.9 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis; pollen yellow. Female flowers absent. Stigma colourless. Ovules 35-58-80 per ovary. Capsule 18-22 mm long. FL. Feb.

DISTRIBUTION (Fig. 48): NELSON: Garibaldi Ridge, Mt Arthur Range (Hoary Head, Mt Arthur, Gordons Pyramid, Mt Olive, Mt Baldy, Mt Patriarch), "Turks Cap Range", Mt Owen Range, northern end of Lookout Range.

HABITAT: In crevices and shallow soil pockets in karst marble outcrops, on marble talus, edges of sinkholes, also similar situations on calcareous siltstones, in *Chionochloa pallens* tussockland in shallow soils, with *Poa colensoi*, *Chionochloa australis*, *Ranunculus lyallii*, *Celmisia spectabilis*, *C. sessiliflora*, *Hebe haastii*, *Dracophyllum prunum*, *Aciphylla ferox*; 1190-1800 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: As with all members of the *G. bellidifolia* group, the plants are polycarpic (with dead flowering stems from previous years' flowering) and the flowering stems are invariably lateral only. The caudex branches are many, prostrate and long, and lie on or just below the soil surface in one direction in a bundle (they usually radiate in *G. decumbens*). The caudices have a shaggy layer of dead leaf bases. The leaves are larger than those found on most *G. bellidifolia* specimens, are not V-shaped in section or

channelled, and have a wider and less distinct petiole than *G. bellidifolia*. The flowers are large, with wide calyx lobes (Fig. 6). The leaves of *G. angustifolia* are matched in their size by those of populations of *G. bellidifolia* from Marlborough (No Mans Creek) and Canterbury (Arthur's Pass). The petiole is wider in most *G. angustifolia* (3.6–5.3–7.6 mm) than in these other large-leaved forms of *G. bellidifolia* (3.5–4.5 mm).

VARIATION: Leaf size varies considerably, probably with soil fertility (Fig. 25).

SPECIMENS EXAMINED: A. P. Druce, Mt Olive, CHR 393808; A. P. Druce, "Turks Cap Range", CHR 395647; A. P. Druce, Hoary Head, CHR 395841; A. P. Druce 1888, Lookout Range, CHR 476152; D. Glennie 6834, Mt Arthur, CHR 530508; D. Glennie 7365, Granity Pass, CHR 559991; D. Glennie 7367b, Sentinel Hill, CHR 559994; D. Glennie 7372, Poverty Basin, CHR 559999; D. Glennie 7418, Garibaldi Ridge, CHR 560049; D. Glennie 7440, Mt Arthur, CHR 560068; D. Glennie 7748, Mt Patriarch, CHR 525241.

CONSERVATION STATUS: Common through its range.

ETYMOLOGY: *Angustifolia* means "narrow leaf", from the tag name A. P. Druce used on herbarium folders at CHR, *Gentiana* "long narrow leaves".

ILLUSTRATION: Fig. 49.

DISCUSSION: Related to *G. bellidifolia* and sympatric with it in the Marino Mountains where *G. angustifolia* occupies sites on or near marble bedrock or on marble gravels, while *G. bellidifolia* grows in peat soils that are presumably more acid and less fertile. The two may be found growing among each other occasionally without intermediates.

Gentianella antarctica (Kirk) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

Basionym: *Gentiana antarctica* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 339 (1895).

Lectotype (here chosen): T. Kirk, Campbell Island, WELT 4729! large plant on right.

Isotype: AK 7330!

≡ *Chionogentias antarctica* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

≡ *Oreophylax antarcticus* (Kirk) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

= *Gentiana concinna* var. *elongata* Hook.f., *Fl. Antarct. 1*: 53 (1844). Holotype: *J. D. Hooker*, Campbell Island, among rocks and in sheltered situations on the tops of the hills, K (photograph seen). Kirk (1895) commented that this is the same as his *G. antarctica* var. *imbricata*.

= *Gentiana concinna* var. *robusta* Hook.f., *Fl. Antarct. 1*: 53 (1844). Holotype: *J. D. Hooker*, Campbell Island, on the hills, K (photograph seen). Isotype: AK 209537!

= *Gentiana antarctica* var. *imbricata* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 339 (1895). Holotype: *T. Kirk*, Campbell Island, WELT 4730! Notes on the type sheet: "I have no doubt that better specimens will prove this to be a new species." Isotype: AK 7331!

DESCRIPTION: Plants monocarpic, probably biennial, height in flower 16–220 mm. Caudex unbranched, 4–13 mm long. Root unbranched, c. 2 mm diameter at stem base. Flowering stems terminal only, largest flowering stem c. 2.5 mm diameter at base (1.1–4.0 mm diameter when dry), stem colour green or tinted crimson, flowering stem leaves 4 pairs per stem, lowest pedicels from halfway up flowering stem. Rosette of leaves distinct from flowering stem leaves, narrowly elliptic, 11–82 mm long, 3.1–17.6 mm wide, green or tinted purple-black or bronze, flat, apex acute to rounded, not recurved or recurved at tips of smaller leaves; margins recurved, thickened; petiole absent or indistinct, c. 5–11 mm long, 1.6–8.8 mm wide at leaf base. Flowering stem leaves almost identical to rosette leaves but shorter and wider. Pedicels one or two per leaf axil, 1.6–4.5 mm long, c. 0.5 mm diameter, 0.46–0.8 mm diameter when dry. Flowers 9–49 per plant, 7–12 mm long. Calyx 5.5–7.6 mm long, hairs at calyx-corolla fusion line present; lobes 4.0–5.9 mm long, 1.2–1.5 mm wide at base, plane, apices acute, margins minutely serrulate, sinus hairs sparse or absent. Corolla (9.5–)10.1–12.6(–14) mm long, white or coloured pink to dark purple with veins colourless or pink to dark purple; tube 3.0–5.5 mm long; lobes 4.6–8.5 mm long, 1.5–2.4(–2.9) mm wide, hairs below sinus absent; nectary 1.6–3.4 mm from corolla base. Filaments 3.4–7.2 mm long from corolla base, 0.5–0.6 mm wide. Anthers 1.0–1.2 mm long, anther wall blue-black, rarely yellow, extrorse at anthesis. Stigma colour unknown. Ovules 7–12–27 per ovary. Capsule 8.0–13.2 mm long. FL. (Dec–)Jan–Feb(–Apr).

DISTRIBUTION: Campbell Island.

HABITAT: Low forest, *Chionochloa antarctica* tussocklands and *Poa littorosa* grasslands, *Marsippospermum gracile* – *Pleurophyllum hookeri* sedgeland on summit fellfields; 0–569 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980).

RECOGNITION: Distinguished from all other New Zealand species by the combination of its erect terminal flowering stem, its flowers on short pedicels, leaves with a thickened and recurved margin, corolla and calyx hairs absent from the sinuses, nectaries distant from the corolla base, and corolla lobes narrow and long.

VARIATION: Shade forms can become attenuated, but usually the plants are so condensed that the stem is not visible in herbarium specimens. Corolla colour variation was described by Godley (1982, p. 410) as ranging from white to tinged with pink, to veined with pink to rose-red all over the corolla surface with darker veins. Similarly, the leaves vary from green with a tinge of brown to partly purple-tinted to purple above and below, the most coloured leaves occurring on plants with the strongest corolla coloration. Plant size varies considerably as a result of soil fertility, from very small (16 mm high) and unbranched in bogs, to large (220 mm high) and with lateral branches, in mineral soils. Rosette leaves on vegetative plants can have very wide petioles, up to 10 mm wide, but are narrower in flowering plants (1.5–2.5 mm wide).

SPECIMENS EXAMINED: *E. J. Godley*, Venus Bog, 1969, CHR 549028 spirit collection; *E. J. Godley*, Azimuth Hill, CHR 549026 spirit collection.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Not threatened.

ETYMOLOGY: Found in the most southern latitudes.

ILLUSTRATION: Godley (1982, fig. 1).

DISCUSSION: The type of *G. antarctica* var. *imbricata* consists of small plants similar to the small ones of those illustrated by Godley (1982). Kirk (1895) distinguishes it by the absence of warts (but these are caused by a fungus as pointed out by Allan 1961),

coriaceous leaves with "strong marginal nerves" (this refers to the recurved margin of *G. antarctica* rather than a nerve), and larger flowers. A flower on the type is 8.5 mm long, within the range for the species. For these reasons, the variety is rejected.

Gentianella antipoda (Kirk) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

Basionym: *Gentiana antipoda* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 340 (1895).

Lectotype (here chosen): *T. Kirk*, Antipodes Islands, Jan 17 1890, with the annotation "stems yellow – flowers white" in red ink in Kirk's hand, WELT SP55079A! whole plant at lower left of sheet. Isolectotype: WELT SP55079B!

≡ *Chionogentias antipoda* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

≡ *Gentiana antipoda* forma *pallida* Kirk, nom. superfl., *Trans. & Proc. New Zealand Inst.* 27: 340 (1895).

= *Gentiana antipoda* forma *rubra* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 341 (1895). Lectotype (here chosen): *T. Kirk*, Antipodes Islands, Jan 17 1890, with the annotation "forma: stems red, corolla red on white with vertical red stripes" in red ink in Kirk's hand. WELT 4731! large plant on left of sheet. Isotypes: AK 7332 & 7333!

DESCRIPTION: Plants monocarpic, biennial, height in flower 35–98–190(–240) mm.

Caudex unbranched or branched (depending on the size of plant), up to 100 mm long.

Flowering stems terminal and lateral, 2–6–20 per plant, 1.5–2.5 mm diameter when dry, yellow or tinted crimson, lateral flowering stems decumbent, flowering stem leaves 5–6 pairs per stem, lowest pedicels from halfway up flowering stem. Rosette of leaves present but not very distinct from flowering stem leaves, leaves narrowly elliptic, 34–39 mm long, 4.8–6.2 mm wide, tinted crimson below or yellow, flat, not recurved, apex acute or rounded; margin thickened; petiole distinct, 3.2–3.5 mm wide. Flowering stem leaves similar to rosette leaves but smaller. Pedicels 1 per leaf axil, 0.8–2.0 mm long, 0.6–0.9 mm diameter. Flowers 73–83 per plant, 5.5–10.5 mm long. Calyx 4.7–8.0 mm long, hairs at calyx-corolla fusion line present; lobes 3.9–6.7 mm long, 0.9–1.3 mm wide at base, green or crimson, plane, apices narrowly acute, margins minutely serrulate, sinus hairs sparse. Corolla 5.5–10.5 mm long, white to purple, with veins uncoloured to purple; tube 1.6–2.9 mm long; lobes 3.9–7.6 mm long, 1.3–2.7 mm wide; hairs below sinus absent; nectary 1.0–1.4 mm from corolla base. Filaments 2.8–6.3 mm long from corolla base, 0.3–0.55 mm wide. Anthers 0.75–1.0 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colour unknown. Ovules 3–4–9 per ovary.

Capsule 2.9–7.2 mm long. FL. Dec–Mar(–Apr).

DISTRIBUTION: Antipodes Islands: Antipodes Island and Bollons Island.

HABITAT: *Poa litorosa* tall tussockland and *Carex ternaria* – *Anisotome antipoda* bogs; 0–366 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980).

RECOGNITION: *G. antipoda* is closest in appearance to *G. antarctica*, *G. cerina* and *G. concinna*. It shares with *G. antarctica* monocarpy, having a thickened and recurved leaf margin, short pedicels, narrowly triangular calyx lobes, narrow corolla lobes, and very small anthers. It differs from *G. antarctica* in having wider leaves, both at the widest point and at the leaf base, longer capsules, more ovules per ovary on average, a longer corolla and longer corolla tube, and narrower filaments. It has smaller anthers than any other Subantarctic Island species.

VARIATION: Most notable is the variation in flower, stem, and leaf colour, described by Kirk (1895) as forma *pallida*, in which stems are yellow and the corolla uniformly white, and forma *rubra*, in which the stems are red, the corolla white with coloured veins. Godley (1982) describes a more complex pattern of colour variation in which anthers are usually blue-black but occasionally yellow, and corolla lobe colour varies from a tinge of pink to completely red. Because of this continuum of colour variation, the lack of geographical or habitat basis for the colour forms, and because the colour variation appears to be a polymorphism based on several genes, Kirk's forms are not recognised here.

SPECIMENS EXAMINED: *E. J. Godley*, Antipodes Island, "bog 1", CHR 549027 spirit collection.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Not threatened.

ETYMOLOGY: Named for the islands where it occurs.

ILLUSTRATION: Godley (1982, fig. 1).

DISCUSSION: Kirk (1895), when he published the name *Gentiana antipoda*, described two formae, forma *pallida* described as "stems yellow, corolla white", and forma *rubra* described as "stems red, corolla white with longitudinal red stripe". These diagnoses match annotations on the type material and allows types of both forms to be selected. Since Kirk, in the same publication, made the autonymic forma *Gentiana cerina* forma *cerina* from Hooker's species *G. cerina*, it is apparent that Kirk was aware of autonymic names. However, Kirk's description of *G. antipoda* in his protologue does not give stem or flower colour, this being reserved for the forma descriptions. This gives the impression that Kirk saw forma *pallida* and forma *rubra* as being the two halves of *G. antipoda*. I have chosen to regard forma *pallida* as a superfluous name (forma *rubra* could alternatively be so regarded).

Kirk (1895), Cheeseman (1906, 1925) and Allan (1961) believed this species to be perennial. Cockayne (1904) suspected it to be biennial, and Godley (1982, p. 407) agreed with this judgement.

Gentianella astonii (Petrie) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

≡ *Gentiana astonii* Petrie, *Trans. & Proc. New Zealand Inst.* 48: 187 (1916). Lectotype (here chosen): B. C. Aston, Valley of Ure R., Marlborough, April 24 1916, ex. herb. Petrie, WELT 4726! branch of plant on right side of sheet. Isolectotypes: WELT 47558! AK 107114!

≡ *Chionogentias astonii* (Petrie) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

DESCRIPTION: Plants perennial, bushy, height in flower 40–150 mm, to 400 mm diameter. Caudex branched, 30–240 mm long. Flowering stems lateral only (but difficult to find terminal rosette), 3–26 per plant, 1.8–2.3 mm diameter, 1.2–2.3 mm diameter when dry, green or purple-black, flowering stem leaves 3–13 pairs per stem, lowest pedicels from near apex of flowering stem. Leaf rosette absent, flowering stem leaves not different from basal leaves. Leaves (8.6–)12.5–32 mm long, 1.1–3.9 mm wide, plane; petiole absent, 1.1–1.5 mm wide at base; apex rounded to acute, not recurved. Pedicels 1 per leaf axil, 0–22 mm long, 0.9–1.4 mm diameter (0.5–1.4 mm diameter when dry). Flowers often solitary on flowering stems, 6–63 per plant, 10–24 mm long. Calyx 5.2–10.0 mm long, hairs at calyx-corolla fusion line present; lobes

3.5–6.2 mm long, 1.1–2.3 mm wide at base, green, sometimes tinted purple-black, plane or recurved, apices acute, margins very finely serrulate or smooth, sinus hairs abundant. Corolla 9.2–15.2 mm long, white, sometimes tinted violet near the apices, veins uncoloured, tube 2.7–5.2 mm long; lobes 6.2–10.8 mm long, 3.9–6.7 mm wide, hairs below sinus absent or present; nectary 1.2–4.3 mm from corolla base, usually with a pocket with an uneven or toothed margin. Filaments 4.0–8.6 mm long from corolla base, 0.5–0.8 mm wide. Anthers 1.1–2.5 mm long, anther wall purple-black or yellow, mouth yellow. Stigma colourless. Ovules 13–30 per ovary. Capsule 7.6–15 mm long. Chromosome number unknown.

KEY TO SUBSPECIES

- | | | | |
|---|--|-------|-----------------------|
| 1 | leaves 8.6–13.1(–25) mm long, 1.1–3.9 mm wide; anthers 1.1–2.0 mm long; ovules 13–28 per ovary | | subsp. <i>arduana</i> |
| | leaves 15.8–32 mm long, (1.4–)1.5–2.8 mm wide; anthers 1.7–2.5 mm long; ovules 27–30 per ovary | | subsp. <i>astonii</i> |

subspecies *arduana* Glenný & Molloy, subsp. nov.

DIAGNOSIS: Ab subspeciei *astonii* nectario marsupiformi margine libera dentata similis, sed foliis minoribus, (8.6–)11.0–13.1–16.0(–25) mm (non 16–32 mm) longis, ad apices latoribus: 2.7–3.9 mm latis, antheris brevioribus 1.1–2.0 mm (non 1.7–2.5 mm) longis, ovulis paucioribus, 13–28 per ovarium (non 27–30) differt.

HOLOTYPE: *D. Glenný* 7488, Marlborough, Chalk Range, 960 m, 18 April 1998, CHR 525472.

DESCRIPTION: Plants 40–110 mm in height. Root 3.1 mm diameter at caudex base. Caudex 30–80 mm long. Flowering stems 3–26 per plant, the largest 1.8–2.3 mm diameter at base, 0.7–1.3(–1.7) mm diameter when dry, green or purple-black; stem leaves 6–13 pairs per stem. Leaf rosette absent. Leaves narrowly to very narrowly elliptic or obovate, (8.6–)11.0–13.1–16.0(–25) mm long, 1.1–2.5–3.9 mm wide, purple at the base, flat or slightly V-shaped in section, margins minutely serrulate or smooth; leaf 0.9–1.2–1.4 mm wide at leaf base; apex rounded to acute. Pedicels (0–)3–18 mm long, 0.9–1.0 mm diameter, 0.52–1.0 mm diameter when dry. Flowers 6–30–52 per plant, 10–20 mm long. Calyx 5.2–6.9–7.1 mm long; lobes 3.5–5.4 mm long, 1.1–1.7 mm

wide at base, green, plane or recurved, lobe margins minutely serrulate, hairs at calyx-corolla fusion line present or absent, sinus hairs absent or sparse. Corolla 9.2–12.5–15.2 mm long, white, usually with violet tinting on the outside and sometimes inside of the corolla lobe apices, tube 3.0–5.2 mm long; lobes 6.2–10.0 mm long, 3.9–6.7 mm wide, toothed only at the apices, margins very finely serrulate or smooth; hairs below sinus absent or present; nectary 1.2–2.2–4.3 mm from corolla base, V-shaped with a pocket or with flaps that are not joined at the base, pocket margins toothed or untoothed. Filaments 4.0–8.6 mm long from corolla base, 0.3–0.5–0.6 mm wide. Anthers 1.1–1.6–2.0 mm long, anther wall blue-black. Ovules 13–19–28 per ovary. Capsule 7.6–15 mm long. FL Mar–Jun(–Oct).

DISTRIBUTION (Fig. 50): MARLBOROUGH: on the seaward side of Weld Cone and the low hills immediately north of the Flaxbourne River mouth Chalk Range, Mead Hill. CANTERBURY: Whalesback Ridge.

HABITAT: Limestone bedrock on cliffs and faces, limestone colluvium, at inland sites with scattered *Podocarpus hallii*, *Coprosma propinqua*, *Chionochloa macra*, *Helichrysum intermedium*, *Leucanthemum vulgare*, *Discaria toumatou*, *Ranunculus insignis*, *Celmisia spectabilis*, *Linum catharticum*, *Epilobium brunnescens*, *Anisotome aromatica*, *Poa colensoi*, *Leptinella pyrethrifolia*, *Schizeilema roughii*, *Anaphalioides bellidioides*, *Carex wakatipu*, and *Campylopus clavatus*; at coastal sites with *Carex wakatipu*, *Hypochoeris radicata*, *Trifolium dubium*, *Microseris scapigera*, and *Oreomyrrhis colensoi*; 0–940 m.

RECOGNITION: Geographically very close to *G. astonii* subsp. *astonii* of the adjacent Waima catchment and shares features such as flat leaves and a toothed nectary flap. It differs from subsp. *astonii* in the purple tinting at the apex of the corolla lobes (without tinting in subsp. *astonii*), by its shorter leaves that are wider at the apex, short anthers (1.1–2.0 mm long, not 1.7–2.5 mm long as in subsp. *astonii*), the smaller number of ovules per ovary (13–28, not 27–30 as in subsp. *astonii*).

SPECIMENS EXAMINED: A. P. Druce, near Flaxbourne River mouth, 500 ft, CHR 277526; A. P. Druce, Mead Hill, CHR 279272; P. J. Garnock-Jones 1996, Weld Cone, CHR 470053; B. B. Given & V. Gamble, Weld Cone, CHR 356737; D. Glenny 7487, Weld Cone, CHR 525471; W. Martin, shady limestone cliff at mouth of Flaxbourne River,

CHR 93296; *R. Mason & D. McQueen*, Chalk Range, CHR 84745; *S. Moore*, Whalesback Ridge, CHR 516238; *G. B. Petterson*, hill north of Flaxbourne Creek mouth, CHR 77907; *G. Simpson*, Chalk Range, CHR 109518; *L. B. Moore & Y. Elder*, Ward Beach, limestone bluff, CHR 233840; *J. S. Thompson and G. Simpson*, Chalk Range, CHR 515356; *W. R. Sykes 556/70*, Limestone Quarry hill, CHR 211891; *A. Wilton*, Chalk Range, CHR 516239.

CONSERVATION STATUS: "Nationally endangered" in the classification of Molloy et al. (2001). Known from four sites in Marlborough and Canterbury but is likely to be at other inland sites (e.g., Limestone Hill). The populations at most of these sites are not threatened by present farming practice as the bluffs on which the subspecies grows are mostly too steep for sheep grazing, and the plants are unpalatable to sheep.

ETYMOLOGY: *Arduana* (steep) refers to the bluffs on which it is usually found.

ILLUSTRATION: Fig. 51.

subspecies *astonii*

DESCRIPTION: Plants 60–150 mm in height, up to 400 mm diameter. Caudex 40–240 mm long, 2.6–5.3 mm diameter at stem base when dry. Flowering stems 5–18 per plant, 1.2–1.9 mm diameter when dry, purple-black; stem leaves 3 pairs per stem. Leaves linear, 15.8–32 mm long, (1.4–)1.5–2.8 mm wide, flat, margins smooth; leaf 1.1–1.5 mm wide at base; apex acute. Pedicels 1.5–22 mm long, 1.2–1.4 mm diameter (0.7–1.4 mm diameter when dry). Flowers 16–63 per plant, 13.5–24 mm long. Calyx 7.0–10.0 mm long, hairs at calyx-corolla fusion line present; lobes 5.2–6.2 mm long, 1.3–2.3 mm wide at base, green tinted purple-black, plane, margins smooth or very finely serrulate, sinus hairs abundant. Corolla 10.4–17 mm long, white, tube 2.7–4.0 mm long; lobes 7.5–10.8 mm long, 4.0–5.7 mm wide, margins finely serrulate, hairs below sinus present (1–2 per sinus); nectary 1.9–2.9 mm from corolla base, widely V-shaped with a flap with an uneven margin (Fig. 7). Filaments 6.0–7.2 mm long from corolla base, 0.7–0.8 mm wide. Anthers 1.7–2.5 mm long, anther wall yellow or blue-black. Ovules 27–30 per ovary. Capsule 8.4–15 mm long. FL. Mar.–Apr(–May).

DISTRIBUTION (Fig. 50): MARLBOROUGH: Waima (Ure) River, Mt Benmore, Washdyke Creek, Mt Alexander.

HABITAT: Limestone bluffs and scree, with *Coprosma propinqua*, *Brachyglottis monroi*, *Dodonaea viscosa*, and *Echium vulgare*; also in *Poa cita* tussockland; 300–1050 m.

RECOGNITION: By the much-branched stem, resulting in bushy plants; by the limestone bluff habitat; by the linear leaves that are no wider than 2.8 mm wide, by the toothed nectary flap that it shares with subsp. *arduana*, and by the smooth calyx and leaf margins.

VARIATION: Anthers in the Waima Valley plants are yellow, while anthers of plants at the other sites are blue-black. The nectary pocket or flap is absent from a Mt Alexander plant. Calyx margins are usually smooth but may be finely serrulate.

SPECIMENS EXAMINED: *B. C. Aston* 882, Ure Basin, CHR 332409; *A. P. Druce*, NW of Mt Benmore, CHR 249199; *A. P. Druce*, Mt Alexander, CHR 401292; *D. R. Given* 66092, Mt Alexander, CHR 175137; *D. Glenny* 6416, Ben More, CHR 509942A; *A. R. Mitchell*, Mt Alexander, CHR 198860; *G. Simpson*, Ure River Gorge, CHR 75730; *C. J. Webb*, Ure River, 1000 ft, CHR 322733; *P. A. Williams*, Washdyke Stream, CHR 404729.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Some populations may be small and under threat, but in the Waima Valley it is reasonably abundant on the limestone bluffs.

ETYMOLOGY: Named for B. C. Aston (1871–1951), chief chemist at the Department of Agriculture in Wellington (Godley 1996).

ILLUSTRATION: Fig. 52, Salmon (1991, p. 222, plates 923 & 924).

Gentianella bellidifolia (Hook.f.) Holub, *Folia Geobot. Phytotax.* 3: 218 (1968).

Basionym: *Gentiana bellidifolia* Hook.f., *Icones Plantarum* t. 635 (1844). Holotype: *J. C. Bidwill*, "on Tongariro, North Island", K (photograph seen).

≡ *Chionogentias bellidifolia* (Hook.f.) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

≡ *Oreophylax bellidifolius* (Hook.f.) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

= *Gentiana flaccida* Petrie, *Trans. & Proc. New Zealand Inst.* 43: 244 (1911).

Holotype: *J. Crosby Smith*, End Peak, Lake Hauroko, WELT 4713!

= *Gentiana bellidifolia* var. *australis* Petrie ex Cheeseman, *Man. New Zealand fl. Ed. 2*

732 (1925). Lectotype (here chosen): *D. P.[etrie]*, Jan 1893, Kelly's Hill c. 4000 ft, Otira River, WELT 47177! plant at lower left of sheet. Isolectotype: WELT 47152!

DESCRIPTION: Plants polycarpic, height in flower 80–130–230(–370) mm. Root 1.2–6 mm diameter at stem base. Caudex unbranched or branched, (15–)23–90 mm long, stolons absent. Flowering stems lateral only, 1–13 per plant, largest flowering stem 1.0–3.2 mm diameter, 0.8–1.4 mm diameter when dry, green, tinted purple-black, or bronze, lateral flowering stems erect or decumbent, stem leaves 2–4 pairs per stem, lowest pedicels from halfway up flowering stem or near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves narrowly elliptic, elliptic, rhomboid, or orbicular, 11–52–100(–140) mm long, (4.0–)4.2–9.5–12.5 mm wide, green or tinted purple-black, channelled, larger leaves V-shaped in section, leaf apex acute to rounded; petiole usually distinct, 7–27 mm long, 0.8–2.3–4.0(–4.6) mm wide at leaf base. Flowering stem leaves elliptic to narrowly ovate. Pedicels 1 per leaf axil, 1–48 mm long, 0.8–1.9 mm diameter, 0.5–0.8 mm diameter when dry. Flowers 1–14–30(–45) per plant, 12–23 mm long, rarely female. Calyx 8.2–9.7–11(–13) mm long; lobes 3.8–6.6–7.0(–8.3) mm long, (1.7–)2.0–3.0–3.6(–4.2) mm wide at base, green or green tinted purple-black, crimson, or brown, plane, lobe apices acute, margins convex, smooth or minutely serrulate, hairs at calyx–corolla fusion line present or absent, hairs at lobe sinuses few. Corolla 15.6–18.6–22.6 mm long, white (in the South Island) or with veins coloured grey-violet (in the North Island), tube 3.4–6.0 mm long; lobes 11.1–17 mm long, 6.3–12.4 mm wide, hairs above sinus present; nectary 0.4–0.85–1.2(–1.4) mm from corolla base. Filaments 7.7–12.5 mm long from corolla base, (0.6–)0.8–1.2–1.4(–2.0) mm wide. Anthers 1.8–2.5–3.0 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules 16–42–60(–68) per ovary, ovary yellow in maturity, rarely turning blue. Capsule 17–20–24 mm long. FL. (Feb–)Mar–Apr.

DISTRIBUTION (Fig. 53): SOUTH AUCKLAND: Pureora. GISBORNE: Huiaurau Range. WELLINGTON: Ruapehu, Kaimanawa, Kaweka, and Ruahine ranges.

MARLBOROUGH: Richmond Range, Raglan Range, Wairau Mountains, Turks Ridge, Inland Kaikoura Mountains, Black Birch Range, Puhi Puhi River. NELSON: Scarlett Range, Allen Range, Cobb Valley, Lockett Range, Peel Range, Arthur Range, Owen Range, Lookout Range, Travers Range, St Arnaud Range, Spencer Mountains, Mt Zetland, Mt Mantell, Glasgow Range. WESTLAND: throughout the Southern Alps on

mountains west of the Main Divide, Paparoa Range, Tuhua Range. CANTERBURY: Lewis Pass, Upper Hope Valley, Upper Hurunui Valley, Upper Clarence Valley, Arthur's Pass, upper catchments of Waimakariri, Rakaia and Rangitata rivers, Mt Somers, Hunter Hills, Two Thumb Range, Mount Cook. OTAGO: Old Woman Range, Old Man Range, Hector Mountains, Rock and Pillar Range, Lammerlaw Range. SOUTHLAND: Garvie Mountains, Eyre Mountains, Fiordland (Murchison Mountains, Tutuko Valley, Caswell Sound, Lake Monk).

HABITAT: Alpine tussocklands and herbfields of *Chionochloa oreophila*, *C. crassiuscula*, *C. flavescens*, and *C. rigida*, with *Poa colensoi*, *Celmisia spectabilis*, *C. sessiliflora*, *C. armstrongii*, *C. haastii*, *C. prorepens*, *Brachyglottis bellidioides*, *Coriaria plumosa*, *Gaultheria crassa*, *Ranunculus lyallii*, *Raoulia hectori*, and *Racomitrium crispulum*; in sedgeland and mossfields in which *Carex gaudichaudiana*, *Schoenus pauciflorus*, and *Sphagnum cristatum* predominate or are commonly present, with *Carpha alpina*, *Oreobolus pectinatus*, *O. pusillus*, *Celmisia glandulosa*, *Dracophyllum muscoides*, *Phyllachne colensoi*, *Pentachondra pumila*, *Dicranoloma robustum*, *Polytrichum commune*, and *Blechnum montanum*; 600–1700 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980; $n = 18$, Post 1983).

RECOGNITION: *G. bellidifolia* has only lateral flowering stems, and is perennial, features shared by all species in the *G. bellidifolia* group and *G. astonii*. It has petiolate leaves that are strongly channelled, decumbent flowering stems, few flowers per flowering stem, and large flowers. *G. bellidifolia* is most similar to *G. serotina* and large Central Otago forms are difficult to tell from that species. *G. bellidifolia* occupies moister habitats, usually at higher altitudes, and it flowers at those altitudes earlier than *G. serotina*. The calyx lobes of *G. bellidifolia* tend to be wider and the margins more convex (Fig. 6). Large-leaved plants (with leaves more than 80 mm long) are uncommon and occur in Marlborough and Canterbury (Fig. 25). They resemble *G. angustifolia* but have narrower, longer and more distinct petioles. In the North Island, *G. bellidifolia* resembles *G. montana* subsp. *ionostigma* closely in size, corolla vein colour, and flower size. The two differ in the following ways: *G. bellidifolia* is perennial, and so has dead flowering stems from previous years' flowering, whereas *G. montana* subsp. *ionostigma* is biennial; *G. bellidifolia* has only lateral flowering stems whereas *G. montana* subsp. *ionostigma* has a terminal flowering stem as well as lateral

stems; *G. bellidifolia* has an uncoloured stigma, whereas *G. montana* subsp. *ionostigma* has a blue or violet stigma. *G. bellidifolia* is very similar to *G. amabilis* and the two grow together in the Otago mountains. For differences see the recognition notes for *G. amabilis*.

VARIATION: North Island specimens have coloured corolla veins, a feature never seen in South Island populations, or in any other species of the *G. bellidifolia* group. *G. bellidifolia* in both main islands is extremely variable in plant height, leaf dimensions (Fig. 25), and floral dimensions. Some of this is habitat induced as the smallest plants grow in oligotrophic alpine cushion bogs. However, some of this variation is genotypic and plants of very different sizes and leaf dimensions are seen growing close to each other or in grading habitats, particularly in Marlborough and Canterbury. Some of the size variation within the species is also regional. Central Otago plants tend to be large. Marlborough and Canterbury have both large and small plants, while plants found west of the Divide in the South Island are the smallest on average. In Marlborough, a distinctive form is found in summit fellfield on Altimarlock, and possibly elsewhere (e.g., Turk Head Saddle). It has long but narrow and very channelled leaves, and the branching pattern is similar to that of *G. decumbens* of Nelson. It possibly deserves taxonomic recognition, but its distribution and whether it grades into other forms in Marlborough is unknown. Burrows & Hobbs (1964) reported that an Arthur's Pass population of *G. bellidifolia* was gynodioecious. This state is rare for this species.

SPECIMENS EXAMINED: *M. J. Bayly* 880, Kaweka Range, CHR 516237; *I. Breitwieser* 2081, Tongariro, CHR 526297; *S. Courtney*, Eric Stream, CHR 526399; *C. Ecroyd*, Kaimanawa Mountains, CHR 526294; *K. Ford* 1/CK, Camp Creek, CHR 526293; *D. Glenny* 6428, Arthur's Pass, CHR 509955; *D. Glenny* 6432, Right Branch Motueka River, CHR 509959; *D. Glenny* 6450, Buckland Peaks, CHR 509977; *D. Glenny* 6899, No Mans Creek, CHR 530572; *D. Glenny* 6925, Trent Saddle, CHR 559482; *D. Glenny* 6931, Harman Pass, CHR 530600; *D. Glenny* 7781, Altimarlock, CHR 525272; *K. Hogan* 1, Altimarlock, CHR 526402; *G. Jane*, Altimarlock, CHR 526406; *P. N. Johnson* 1373, Old Man Range, CHR 511801; *P. N. Johnson* 1398, Livingstone Mountains, CHR 526298; *B. Rance*, Takitimu Mountains, CHR 526414; *S. Wagstaff* 97-130, Ruahine Range, CHR 526418; *A. Wilton*, Ruapehu, unvouchered.

CONSERVATION STATUS: Widespread and common.

ETYMOLOGY: Leaves resemble *Bellis*.

ILLUSTRATIONS: Fig. 29; Cheeseman (1914, p. 2, plate 140); Wilson (1996, p. 225, fig. 59).

DISCUSSION: Cheeseman (1925, p. 732) states that "The plate in the *Icones Plantarum* ... must be taken as the type". This is unnecessary as Hooker's specimen is held at Kew and matches the plate in *Icones Plantarum*.

Gentiana bellidifolia var. *australis* was published by Cheeseman (1925), citing Petrie as the author, probably as a result of Cheeseman seeing specimens in Petrie's herbarium annotated "var. *australis* var. nov." and in one case "a good var. at least". I have chosen a lectotype from six syntypes that are all from Petrie's herbarium and have been identified by Petrie as var. *australis*, usually with the annotation "var. nov". The six syntypes are from Mt Peel, Gordons Knob, Mt Frederick, and Buckland Peaks in Nelson, Mon Sex Millia in Canterbury, Kelly Range in Westland, and Bold Peak and Rock and Pillar Range in Otago. Cheeseman gives the distribution as "high peaks on the mountains of the western coast of the South Island, from Karamea to Westport, Westland, and South West Otago. His diagnosis of the variety is: "Stouter, often forming short dense patches 3–5 in diam. Flowers abundantly produced, large, often quite 1 in. diameter." Allan (1961) notes that "Specimens collected by Petrie and others placed in herbaria under this name \pm agree with the above diagnosis". Druce (1974, p. 425) claimed "it certainly is a distinct species". I am unable to agree with any of these authors that populations of *G. bellidifolia* west of the Divide in the South Island are made up of plants larger than those elsewhere, in fact the opposite is true, as reflected in leaf sizes shown in Fig. 25. Westland specimens tend to be smaller than any others, particularly than the large variants of Nelson and Central Otago, and smaller than plants from North Island populations. Westland plants differ from North Island populations only by their lack of coloured veins in the corolla, a feature shared by all South Island plants.

Gentianella calcis Glenny & Molloy, sp. nov.

DIAGNOSIS: Ab *Gentianella astonii* foliis longioribus (30–83 mm longis, non 9–32 mm longis), minusve plicata, et apices recurvibus differt.

HOLOTYPE: *B. Molloy*, Otago, Waitaki Valley, Awahokomo Creek, true left, limestone tower, 3 April 1995, CHR 529113.

DESCRIPTION: Plants polycarpic, 50–200 mm high when in flower. Flowering stems decumbent, lateral only, 1–5 per plant, the largest 1.1–1.8 mm diameter at base, 0.5–1.6 mm diameter when dry, purple-black; leaves 4–7 pairs per stem. Leaf rosette present and distinct from flowering stem leaves; leaves linear, very narrowly elliptic, narrowly elliptic, or very narrowly obovate, 30–83 mm long, 2.6–8.8 mm wide, green, V-shaped in section, apex acute or rounded, recurved; margins minutely serrulate; petiole not distinct or distinct and then 14–32(–50) mm long, leaf 0.7–1.5 mm wide at the base. Pedicels 3.5–27 mm long, 0.75–1.0 mm diameter, 0.4–0.7 mm diameter when dry. Flowers 7–78 per plant, 12–18 mm long. Calyx green tinted purple-black or red-brown, 5.6–14.1 mm long, hairs at calyx-corolla fusion line present; lobes 4.3–10.2 mm long, 1.3–2.5 mm wide at the base, plane to recurved, apices acute, margins minutely serrulate, rarely smooth, sinus hairs present. Corolla 9.4–17.1 mm long, white, veins uncoloured or purple; tube 2.8–5.1 mm long; lobes 6.6–14.3 mm long, 3.6–9.0 mm wide, hairs below sinus absent or present, when present straight or curly; nectary 0.8–2.2 mm from corolla base, V-shaped to pocket-like, with or without a smooth-margined flap. Filaments 5.4–9.4 mm long from corolla base, 0.4–0.9 mm wide. Anthers 1.5–3.1 mm long, wall blue-black, mouth yellow; pollen yellow. Stigma colourless. Ovules 9–35 per ovary. Ovary becoming blue or bluish-purple after flowering or colour unknown. Capsule 8.0–17.5 mm long.

KEY TO SUBSPECIES

- 1 corolla with purple veins; South Canterbury near Albury subsp. *manahune*
corolla entirely white 2
- 2 corolla 9.4–11.5 mm long; North Canterbury subsp. *waipara*
corolla 13.5–19 mm long 3
- 3 leaves 42–75 mm long, 4.4–8.8 mm wide; South Canterbury subsp. *taiko*
leaves 68–83 mm long, 2.6–4.1 mm wide; Otago subsp. *calcis*

subspecies *calcis*

DESCRIPTION: Plants in flower 140–200 mm high. Flowering stems 1–5 per plant; largest flowering stems c. 1.8 mm diameter at base, 1.2–1.6 mm diameter when dry, purple-black; flowering stem leaves 4 pairs per stem, lowest pedicels from near apex of flowering stem. Rosette leaves linear, 68–83 mm long, 2.6–4.1 mm wide, green, V-shaped in section; apex acute, recurved; margins minutely serrulate or smooth; petiole not distinct, leaf 1.1–1.6 mm wide at leaf base. Flowering stem leaves linear, slightly recurved. Pedicels 3.5–14 mm long, 0.8–1.0 mm diameter, 0.5–0.6 mm diameter when dry. Flowers 9–28(–78) per plant, 15–18 mm long. Calyx 7.5–14.1 mm long, green tinted purple-black; lobes 4.6–10.2 mm long, 1.9–2.5 mm wide at base, plane to somewhat recurved. Corolla 13.5–17.1 mm long, veins colourless; tube 3.4–5.1 mm long; lobes 10.0–12.3 mm long, 6.2–9.0 mm wide, margins toothed, hairs below sinus absent or rarely present and then straight; nectary 0.9–1.6 mm from corolla base, V-shaped to pocket-like, flap margin smooth. Filaments 6.5–8.6 mm long from corolla base, 0.6–0.9 mm wide. Anthers 1.9–3.1 mm long, extrorse at anthesis. Ovules (9–)14–35 per ovary. Ovary becoming bluish-purple after flowering. Capsule 13.0–17.5 mm long.

DISTRIBUTION: OTAGO: near Kurow, base of St Mary Range, Awahokomo Valley.

HABITAT: Plateau on top of bluff, in hollows and fissures with shallow limestone debris, with *Convolvulus vericundus*, *Crassula albida*, *Hieracium pilosella*, *Ischnocarpus exilis*, *Poa spania*, *Raoulia beauverdii*, *Sedum acre*, *Syntrichia* sp., *Chondropsis semiviridis*, *Wahlenbergia* sp.; 480 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980 as *Gentiana astonii*, Dawson & Beuzenberg 2000).

RECOGNITION: The subspecies of *G. calcis* are compared in Table 49.

Table 49 Comparison of subspecies of *Gentianella calcis*.

	ssp. <i>waipara</i>	ssp. <i>manahune</i>	ssp. <i>taiko</i>	ssp. <i>calcis</i>
Bush / rosette form	rosette	bush	rosette	rosette
Leaf length (mm)	58–56.3–78	30–44.0–60	42–47.1–75	69–72.5–83
Leaf width (mm)	3.0–6.0–6.9	2.8–3.5–4.1	4.4–6.1–8.8	2.6–3.4–4.1
Leaf folding	very strong	weak	weak	strong
Corolla colour	white, veins colourless	white, veins purple	white, veins colourless	white, veins colourless
Corolla sinus hairs	absent or sparse	present, curled	present, straight	absent or sparse

SPECIMENS EXAMINED: *P. J. de Lange* 2796 & *G. M. Crowcroft*, Awahokomo Bluff, AK 490856; *D. Glenny* 8234, Awahokomo, CHR 560262.

CONSERVATION STATUS: "Nationally critical" in the classification of Molloy et al. (2001) as the subspecies is known from one population of fewer than 250 plants. The numbers of plants present seems to vary year to year, possibly because of grazing pressure by rabbits and variation in summer dryness. The site has the sole populations of several rare species (Molloy et al. 1999), and is therefore an important one for conservation.

ETYMOLOGY: *Calcis* means "of limestone" and applies to the habitat of *G. calcis*.

ILLUSTRATION: Fig. 54.

subspecies *manahune* Glenny & Molloy, subsp. nov.

DIAGNOSIS: Ab subspeciebus ceteris caule florifero amplissime ramoso, caudice brevi, foliis tantum subcarinatis, 30–60 mm longis, 2.8–4.1 mm latis, apice foliari leniter recurvo, villis in sinibus calycinis, corolla 12–14 mm longa, nervis purpurascensibus ornata, marginibus subdentatis, nectario non marsupiformi distinguenda.

HOLOTYPE: *D. Glenny* 8232 & *B. Molloy*, Manahune Station, CHR 560259.

DESCRIPTION: Plants in flower c. 50 mm high. Flowering stems 1–3 per plant; largest flowering stem 1.3–1.4 mm diameter at base, 0.5–0.7 mm diameter when dry, purple-black, leaves 8 pairs per stem, lowest pedicels from halfway along flowering stems. Rosette leaves linear to very narrowly elliptic to very narrowly obovate, 30–60 mm long, 2.8–4.1 mm wide, green, V-shaped in section, recurved at the acute apex; margins finely serrulate; petiole distinct, 14–32 mm long, 0.7–1.1 mm wide at leaf base. Pedicels 6.5–12 mm long, 0.75–0.9 mm diameter, 0.4–0.5 mm diameter when dry. Flowers 24–42 per plant, 12–15 mm long. Calyx 6.8–7.0 mm long; lobes 4.3–5.7 mm long, c. 1.5 mm wide at base, green tinted purple-black, apices acute, recurved, margins minutely serrulate, sinus hairs c. 2 per sinus. Corolla 11.7–13.8 mm long, veins purple; tube 3.1–4.3 mm long; lobes 7.7–9.5 mm long, 5.4–6.0 mm wide, lobe apices slightly toothed, hairs below sinus present, curly; nectary 2.0–2.1 mm from corolla base, V-shaped, deep but without a flap. Filaments 6.6–8.1 mm long from corolla base, 0.45–0.6 mm wide. Anthers 1.75–2.0 mm long. Ovules 15–21 per ovary. Ovary becoming blue at the apex after fertilisation. Capsule 8.0–11.5 mm long. Seeds c. 0.70 × 0.55 mm. FL. May.

DISTRIBUTION: CANTERBURY: Albury, Manahune Station.

HABITAT: Ridge of limestone escarpment, in cracks in limestone, with *Festuca rubra*, *Coprosma propinqua*, *Poa pratensis*, *P. colensoi*, *Gingidia enysii*, *Oreomyrrhis rigida*, *Holcus lanatus*, *Hieracium pilosella*, *Melicytus alpinus*, *Geranium* aff. *sessiliflorum*, *Asplenium lyallii*, and *Colobanthus* aff. *strictus*; c. 440 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: In common with all other subspecies of *G. calcis*, this subspecies has lateral, decumbent flowering stems. Its leaves are very narrowly elliptic and they are V-shaped in section and recurved at the tips. This is the only subspecies of *G. calcis* that has purple veins in the corolla.

VARIATION: Known from only one population.

SPECIMENS EXAMINED: *B. Molloy*, 29/5/92, Manahune Station, CHR 542276.

CONSERVATION STATUS: "Nationally critical" in the classification of Molloy et al. (2001) as it is known from a single population of fewer than 250 plants. Thirty-five plants were seen in May 1999. Many parts of the escarpment that have suitable habitat could not be searched because of their steepness, and it is likely the population consists of c. 100 plants. Threatened by adventives such as *Festuca rubra*.

ETYMOLOGY: Named for the station where the subspecies is found. "Manahune" means limestone bluff.

ILLUSTRATION: Fig. 55.

DISCUSSION: The subspecies has been described from limited material because of the rarity of the species.

subspecies *taiko* Glenny & Molloy, subsp. nov.

DIAGNOSIS: Ab subspeciebus ceteris caule florifero sparse ramoso, caudice et longo et ramoso, foliis tantum subcarinatis, 42–75 mm longis, 4.4–7.8(–8.8) mm latis, apice foliari recurvo, villis in sinibus calycinis, corolla 14.6–19.0 mm longa, alba marginibus dentatis, nectario marsupiformi margine libera integra distinguenda.

HOLOTYPE: *B. Molloy*, South Canterbury, Limestone Valley Road, 24 April 1992, CHR 529111.

DESCRIPTION: Plants not bushy, height in flower c. 50 mm. Flowering stems 1–5 per plant, 19–41 mm long; largest flowering stem 1.1–1.4 mm diameter at base, 0.60–1.4 mm diameter when dry, purple-black, leaves 5–7 pairs per stem, lowest pedicels from near base of flowering stem. Rosette leaves narrowly elliptic, 42–75 mm long, 4.4–7.8(–8.8) mm wide, green, slightly V-shaped in section, slightly recurved, apex acute to rounded; margins minutely serrulate; petiole distinct, 15–18(–50) mm long, 0.8–2.1 mm wide at leaf base. Flowering stem leaves recurved. Pedicels 1 per leaf axil, 27 mm long, 0.9 mm diameter, 0.5–0.6 mm diameter when dry. Flowers 28–65 per plant, 1–18 per flowering stem, 16–18 mm long. Calyx 6.8–9.8 mm long, green tinted purple-black; lobes 4.5–7.2 mm long, 1.3–1.8 mm wide at base, strongly recurved, apices acute, margins minutely serrulate, sinus hairs 1–3 per sinus. Corolla

(11.7–)14.6–19.0 mm long, veins colourless; tube (3.6–)4.2–4.7 mm long; lobes (7.8–)9.2–14.3 mm long, (3.6–)4.8–6.9 mm wide, usually toothed, hairs below sinus present, straight; nectary 0.8–2.2 mm from corolla base, V-shaped to pocket-like with a distinct smooth-margined flap. Filaments (6.5–)7.3–9.4 mm long from corolla base, 0.40–0.65 mm wide. Anthers 1.5–2.2 mm long. Ovules 14–24 per ovary. Capsule 13.0–16.5 mm long. Seeds 1.1–1.4 × 0.9–1.0 mm. FL. Apr–May.

DISTRIBUTION: CANTERBURY: Limestone escarpment to the east of Limestone Valley Road near Taiko.

HABITAT: On limestone boulders on colluvial hillslope below an escarpment in *Festuca rubra*, *Holcus lanatus*, *Cirsium californicum*, and *Achillea millefolium* grassland; also on a shaded ledge on the same escarpment with *Brachyscome sinclairii*, *Colobanthus brevisepalus*, *Craspedia* sp., *Festuca rubra*, *Hieracium pilosella*, *Hypnum cupressiforme*, *Lagenifera* sp., *Lembophyllum divulsum*, *Linum catharticum*, *Medicago lupulina*, *Orthotrichum cupulatum*, *Poa colensoi*, *Porella elegantula*, and *Sedum acre*; 180–240 m.

CHROMOSOME NUMBER: $2n = 36$ (Dawson & Beuzenberg 2000).

RECOGNITION: Of the subspecies of *G. astonii* this one has the widest leaves (4.4–8.8 mm). The secondary branching of the flowering stems is sparse. The leaves are long and only slightly V-shaped in section, the corolla is large (14.6–19 mm long) and uniformly white and the nectary has a flap with an untoothed margin.

SPECIMENS EXAMINED: *D. Glenny* 8233, Limestone Valley Road, CHR 560260; *B. H. Macmillan* 73/481, at south end of escarpment above junction of Limestone Valley Road and McLeods Road, CHR 256518; *A. E. Woodhouse*, "Limestone Valley, off Taiko Flat", CHR 191742.

CONSERVATION STATUS: "Nationally critical" in the classification of Molloy et al. (2001), as the subspecies is currently known from one population of fewer than 250 plants. This site is within an area under the protection of a QE II Conservation Trust conservation covenant. The other site at the south end of the escarpment has not been revisited since Macmillan's collection was made in 1973.

ETYMOLOGY: Named for the locality at which it has been found.

ILLUSTRATIONS: None.

subspecies *waipara* Glenny & Molloy, subsp. nov.

DIAGNOSIS: Ab subspeciebus ceteris caule florifero sparse ramoso, foliis carinatis, 58–78 mm longis, lamina 4.8–6.9 mm lata, apice foliari recurvo, villis in sinibus calycinis nullis, corolla alba marginibus integris, nectario non marsupiformi distinguenda.

HOLOTYPE: *B. Molloy*, North Canterbury, Waipara Gorge, Ridge to Mt Brown, 10 April 1992, CHR 529112.

DESCRIPTION: Plants in flower 80–150 mm high. Flowering stems up to 4 per plant, the largest 2.3 mm diameter at base, 0.9–1.3 mm diameter when dry; stem leaves c. 6 pairs, lowest pedicels from near base of flowering stem. Rosette leaves linear, 58–78 mm long, 3.0–6.9 mm wide, green or tinted purple-black at base, V-shaped in section, recurved; margins minutely serrulate; petiole distinct, 1.1–1.8 mm wide at leaf base; apex rounded. Flowering stem leaves linear. Pedicels c. 19 mm long, c. 0.8 mm diameter, 0.52–0.66 mm diameter when dry. Flowers 7–25 per plant, c. 15 mm long. Calyx 5.6–10.0 mm long, green, or red-brown, sometimes purple-black on the margins; lobes 4.5–8.1 mm long, 1.3–1.6 mm wide at base, apices acute, plane or recurved, margins minutely serrulate, occasionally smooth, sinus hairs sparse. Corolla 9.4–14 mm long, veins colourless; tube 2.8–4.0 mm long; lobes 6.6–10.0 mm long, 4.5–5.4 mm wide, margins finely serrulate or smooth; hairs below sinus absent or present and sparse; nectary 1.2–1.4 mm from corolla base, with or without a pocket, pocket margins smooth. Filaments 5.4–7.6 mm long from corolla base, 0.4–0.7 mm wide. Anthers 1.6–2.2 mm long. Ovules 11–28 per ovary. Capsule 9.3–11.6 mm long.

DISTRIBUTION: CANTERBURY: Whiterock, Mt Brown, Weka Pass, Waipara River, North and South Dean.

HABITAT: Limestone ridge, in pockets in limestone bedrock in sparse *Festuca rubra* – *Echium vulgare* grassland, with *Linum catharticum*, *Heliohebe raoulii* subsp. *maccaskillii*, *Hieracium pilosella*, *Hypochoeris radicata*, *Medicago lupulina*, *Poa*

acicularifolia, *P. colensoi*, *Gingidia enysii*, *Sedum acre*, and *Celmisia gracilentia*;
230–490 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: This subspecies belongs in *G. calcis* as shown by its polycarpy, the secondary branching of the flowering stems, the lateral flowering stems, and the serrulate leaf and calyx margins. It is distinguished by the following combination of characters: secondary branching of the flowering stems is sparse (as in *G. calcis* subsp. *calcis* and subsp. *taiko*), the leaves are long (58–78 mm) as in *G. calcis* subsp. *calcis*, relatively wide at the apices (4.8–6.9 mm) as in *G. calcis* subsp. *taiko*, the leaf apex is slightly recurved, the leaves are V-shaped in section, the corolla white with smooth lobe margins, and the nectary lacks a flap, unlike the other three subspecies of *G. calcis*. It is probably most closely related to subsp. *manahune* of South Canterbury, being similar in its leaf dimensions and the degree of branching of the stems. From subsp. *manahune* it differs in the absence of calyx sinus hairs, its longer leaves (58–78 mm, not 30–60 mm) and a more sparsely branched structure. To the north, the closest relative is *G. astonii* subsp. *arduana*, from which it differs in having smaller plants due to more sparsely branched structure stems, a more prostrate habit, longer and more strongly folded leaves, and an absence of calyx sinus hairs.

VARIATION: Too few specimens are available to describe any variation.

SPECIMENS EXAMINED: A. P. Druce, Weka Pass, CHR 394403; D. Glenny 7456, Mt Brown, CHR 256518; A. J. Healy, Mt Donald, CHR 33424; A. W. Robertson, South Dean, CHR 419784.

CONSERVATION STATUS: "Nationally critical" in the classification of Molloy et al. (2001), as the subspecies is known from few sites and is in small numbers even at what appears to be the main site at Mt Brown. It is in serious decline and has become extinct at some sites due to crowding, mainly by *Festuca rubra*. It appears to have become extinct at Weka Pass where Brian Molloy and I could not find it in 1998, and at Mt Donald where in 1998 we failed to find this subspecies at the site of Healy's collection made in 1941. Of the six limestone taxa of the *G. astonii* group, this one is most seriously in decline.

ETYMOLOGY: Confined to the Waipara River catchment.

ILLUSTRATION: Fig. 34.

Gentianella cerina (Hook.f.) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 62 (1993).

Basionym: *Gentiana cerina* Hook.f., *Fl. Antarct. 1*: 54 (1844). Holotype: J. D. Hooker, Auckland Islands, K (photograph seen). The sheet with the label "1457 Lord Auckland Group" appears to be the type.

≡ *Chionogentias cerina* (Hook.f.) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

= *Gentiana campbelli* Hombr. & Jacquinot ex Decne. *Voyage au Pôle Sud* 22 (1853).

= *Gentiana cerina* forma *suberecta* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 339 (1895). Lectotype (here chosen): T. Kirk, Adams Island, Carnley Harbour, "on sheltered places on the hill sides, 100–900 ft", WELT 4728! branch of a plant in upper left of sheet. Isotypes: AK 7327!, K (photograph seen).

≡ *Gentiana cerina* var. *suberecta* (Kirk) Cheeseman, *Man. New Zealand fl.* 455 (1906).

DESCRIPTION: Plants polycarpic, height in flower 90–170 mm. Caudex unbranched or branched, 110–200 mm long. Flowering stems terminal only or terminal and lateral, 3–12 per plant, 1.1–3.1 mm diameter when dry, lateral flowering stems decumbent, flowering stem leaves 3–4 pairs per stem (not applicable in cases where no rosette is present on multiply-branched plants), lowest pedicels from halfway up flowering stem to near apex of flowering stem. Rosette of leaves absent, not very distinct, or distinct from flowering plants leaves; leaves narrowly elliptic, 36.6–53.1 mm long, 8.4–12.6 mm wide, flat, not recurved, margins thickened, apex rounded and retuse; petiole distinct, 11–13 mm long, 4.7–6.3 mm wide at leaf base. Flowering stem leaves the same but smaller. Pedicels 1 or 2 per leaf axil, 6.2–17.8 mm long, 1.2–1.3 mm diameter, 0.7–1.0 mm diameter when dry. Flowers 15 to more than 100 per plant, 9.9–14.1 mm long. Calyx 9.3–12.2 mm long, hairs at calyx-corolla fusion line present; lobes 7.5–10.3 mm long, 2.4–3.4 mm wide at base, plane, apices obtuse (widest near the apex), margins smooth, sinus hairs absent. Corolla 8.4–11.8 mm long, white or tinted red to purple, veins colourless or purple; tube 2.1–4.4 mm long; lobes 6.3–8.8 mm long, 3.8–5.0 mm wide, hairs below sinus absent or present; nectary 1.2–1.5 mm from corolla base. Filaments 4.9–6.9 mm long from corolla base, 0.70–0.85 mm wide. Anthers 0.9–1.7 mm long, extrorse at anthesis; pollen yellow. Stigma purple or colourless. Ovules 13–37 per

ovary. Capsule 6.5–9.5–12 mm long. FL. (Dec–)Jan–Mar(–Apr).

DISTRIBUTION: Auckland Islands: Auckland Island, Enderby Island, Adams Island, Disappointment Island.

HABITAT: Coastal turflands, low forest, *Chionochloa antarctica* tussocklands and *Poa littorosa* grasslands, *Marsippospermum gracile* and *Pleurophyllum hookeri* sedgeland or bare ground on summit fellfields, with *Astelia linearis*, *Coprosma cuneata*, *Geranium microphyllum*, *Hebe benthamii*, *Hierochloa fusca*, *Marchantia berteroana*, *Polystichum vestitum*, *Ranunculus pinguis*, and *Stellaria decipiens*; 0–600 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: Differences from the other Auckland Islands species, *G. concinna*, are listed in Table 11.

VARIATION: Varies in the colour of the corolla, leaves and stems as described.

SPECIMENS EXAMINED: *C. Meurk*, Auckland Is., CHR 510017.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Not threatened.

ETYMOLOGY: *Cerina* means "waxy yellow", perhaps referring to the colour of the flowers when dried.

ILLUSTRATIONS: Hooker (1844a, plate 36) has an excellent illustration of the species done by J. N. Fitch; Johnson (1997, p. 165); Metcalf (1993, plate 91) shows the vivid flower colour.

DISCUSSION: Kirk's var. *suberecta* is not recognised here. In my opinion it describes merely an inland, more erect, environmentally induced form.

Gentianella chathamica (Cheeseman) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 62 (1993).

Basionym: *Gentiana chathamica* Cheeseman, *Man. N. Z. fl.* 449 (1906). Lectotype (here chosen): F. A. D. Cox, Peaty swamps, Chatham Islands, AK 7181! plant on right of sheet. Sheet annotated as lectotype by L. M. Cranwell, Dec. 1941.

≡ *Chionogentias chathamica* (Cheeseman) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

= *Gentiana pleurogynoides* var. *umbellata* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 335 (1895) pro parte. Lectotype (here chosen): F. A. D. Cox, Chatham Islands, WELT 47795! right-hand plant on sheet.

DESCRIPTION: Plants monocarpic, probably biennial, height in flower (25–)90–240(–300) mm. Caudex unbranched, stolons absent. Root 0.7–3.3 mm diameter at stem base. Flowering stems terminal only or terminal and lateral, 1–5(–9) per plant, largest flowering stem 2.1–2.3 mm diameter at base, 0.9–3.4 mm diameter when dry, stems tinted crimson, lateral flowering stems erect, flowering stem leaves 1–3 pairs per stem, lowest pedicels from near base of flowering stem. Rosette of leaves distinct to not very distinct from flowering stem leaves; leaves ovate, elliptic or orbicular, 21–44 mm long, 4.8–15.2 mm wide, tinted crimson above and below, flat or V-shaped in section, not recurved, apex acute or rounded; petiole indistinct to distinct, 3–20 mm long, 0.6–3.0 mm wide. Flowering stem leaves ovate, sessile. Pedicels 1 per leaf axil, 3.5–20 mm long, 0.5–0.8 mm diameter, 0.37–0.70 mm diameter when dry. Flowers 5–50(–70) per plant, 6.0–12.0 mm long. Calyx 5.8–7.9 mm long, green, hairs at calyx-corolla fusion line present; lobes 4.2–6.1 mm long, 1.0–2.3 mm wide at base, plane, apices acute or obtuse, margins smooth, sinus hairs absent or sparse. Corolla 7.0–11.8 mm long, white or coloured, veins coloured or uncoloured; tube 2.0–3.2 mm long; lobes 5.0–8.6 mm long, 2.1–5.2 mm wide, hairs below sinus absent or present; nectary 0.2–1.2 mm from corolla base. Filaments 3.9–6.6 mm long from corolla base, 0.3–0.7 mm wide. Anthers 0.5–1.4 mm long, anther wall purple-red to purple-black, mouth yellow or orange-red, introrse or extrorse at anthesis; pollen yellow to pale orange. Female flowers absent. Stigma colourless or purple. Ovules 13–60 per ovary. Capsule 6.5–12.5 mm long.

KEY TO SUBSPECIES

- 1 plants usually (in c. 70% of plants) with only one flowering stem; ovules 25–60 per ovary; anthers 0.5–1.4 mm long; stigma colourless; Chatham and Pitt Islands, bracken fernland and shrublands subsp. *chathamica*

plants uncommonly (23% of plants) with only one flowering stem; ovules 9–29 per ovary; anthers 0.4–1.1 mm long; stigma crimson, blue, or purple; North Island, forest and forest margins, rarely in tussockland subsp. *nemorosa*

subspecies *chathamica*

DESCRIPTION: Plants in flower 90–125–235 mm high. Root 1.0–3.3 mm diameter at stem base. Flowering stems terminal 1–3(–15) per plant, largest flowering stem 2.1–2.3 mm diameter at base, 0.9–3.4 mm diameter when dry, flowering stem leaves 1–3 pairs per stem. Rosette leaves ovate, 21–27.2–31 mm long, 7.0–9.4–11.5(–22) mm wide; petiole distinct, c. 9.5 mm long, 0.6–3.0 mm wide. Pedicels 1 per axil, 5–20 mm long, 0.5–0.8 mm diameter, 0.37–0.46 mm diameter when dry. Flowers 5–28–50 per plant, 6–12 mm long. Calyx 4.6–6.3–7.5 mm long, hairs at calyx-corolla fusion line present; lobes 4.7–5.7 mm long, 1.5–1.8–2.2(–2.5) mm wide at base, apices acute or obtuse, margins smooth, sinus hairs absent or sparse. Corolla (5.1–)7.5–8.3–11.8 mm long, white, with crimson tinting, and/or with veins coloured crimson; tube 2.5–3.2 mm long; lobes 5.0–8.6 mm long, 2.7–5.2 mm wide, hairs below sinus present; nectary 0.9–1.2 mm from corolla base. Filaments (2.3–)3.9–4.8–6.6 mm long from corolla base, 0.4–0.7 mm wide. Anthers 0.5–1.1–1.4 mm long, anther wall purple-red, mouth yellow or orange-red, introrse or extrorse at anthesis, pollen pale orange. Stigma colourless. Ovules 22–37–60 per ovary. Capsule 6.7–9.6–12.5 mm long. FL. (Aug–)Sep–Feb.

DISTRIBUTION: Chatham Island, Pitt Island.

HABITAT: *Pteridium esculentum* fernland and shrub fernland, with *Gleichenia dicarpa*, *Hypochoeris radicata*, *Anthoxanthum odoratum*, *Ulex europaeus*, *Leucopogon parviflorus*, *Cyathodes robusta*, *Olearia chathamica*, and *Dracophyllum paludosum*. "Scattered over peaty country in shrublands and rush-shrubland but avoids tall *Sporodanthus* stands. It is frequent following recent fires on some sites" (Given & Williams 1985, p. 87); 5–140 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980).

RECOGNITION: The only gentian present on the Chatham Islands. Characterised by its terminal flowering stem and, when present, smaller lateral stems, crimson flowering

stems, purple corolla veins, small flowers (6–12 mm long) and small anthers (0.5–1.4 mm long). Differs from subsp. *nemorosa* by its paucity of lateral flowering stems, with c. 70% of plants having only a single terminal flowering stem. It has smaller anthers, but a high number of ovules, 22–60 per ovary. The open brackenland habitat differs from the forest and forest margin habitat of subsp. *nemorosa*.

SPECIMENS EXAMINED: *P. J. de Lange* CH21, Chatham Island, CHR 510011; *D. Glenny* 7152, Waimahana Creek, CHR 559759; *D. Glenny* 7260, Tuku-a-tamatea River, CHR 526291; *W. Sykes* 497/93, near Awatotara River, CHR 496871.

CONSERVATION STATUS: Described as "rare" in Given & Williams (1985, p. 87) but abundant on the southern tablelands of Chatham Island where it seems to benefit from the disturbance of current farming practice, but would be threatened there by more intensive farm development or the peat mining that was proposed in the 1980s. Present in reserves on Chatham Island. "Range restricted" in the classification of Molloy et al. (2001).

ETYMOLOGY: From the Chatham Islands.

ILLUSTRATION: Cheeseman (1914, vol. 2, p. 138).

DISCUSSION: A subspecies with an unusual pollination system seen in its introrse and small anthers described by Webb & Pearson (1993). In contrast to *G. chathamica* subsp. *nemorosa* and other taxa with small anthers such as *G. antarctica*, *G. antipoda* *G. gibbsii*, and *G. lineata*, the ovule number is relatively high. The flowering season appears to be a very long one with plants often collected in flower as early as September.

subspecies *nemorosa* Glenny subsp. nov.

DIAGNOSIS: Ab subspecie *chathamicae* pluribus caulis floriferi, ovulis 9–29 per ovarium, antheris 0.4–0.74–1.1 mm longis, stigmatе purpureo, statione sylvestri vel ad marginem sylvarum distinguenda.

HOLOTYPE: *W. B. Shaw*, Urewera National Park, NE of Lake Waikareiti, "Sopps Clearing", NZMS 260 W18 743705, 960 m, 21 February 1999, CHR 565235 (Fig. 56).

DESCRIPTION: Plants in flower 25–100–210(–300) mm tall. Root c. 0.7 mm diameter at stem base. Caudex unbranched. Flowering stems 1–7(–18) per plant, largest flowering stem c. 1.6 mm diameter at base, 1.3–1.8 mm diameter when dry, flowering stem leaves 1–2 pairs per stem. Rosette leaves elliptic, orbicular, or ovate, leaf apex rounded, 18–26.3–44 mm long, (3.6–)4.8–9.3–15.2 mm wide, green or tinted crimson below, flat, not recurved. Petiole indistinct, c. 3–20 mm long, 0.9–1.4(–2.2) mm wide at leaf base. Flowering stem leaves ovate, sessile. Pedicels 1 per leaf axil, 3.5–17 mm long, c. 0.8 mm diameter, 0.5–0.7 mm diameter when dry. Flowers 6–39(–70) per plant, 6.0–8.8 mm long. Calyx 5.8–7.9 mm long; lobes 4.2–6.1 mm long, 1.2–1.7–2.1(–2.5) mm wide at base, apices acute, margins minutely serrulate, hairs at calyx–corolla fusion line present, sinus hairs absent. Corolla 4.5–7.1–9.8 mm long, white with veins crimson; tube 2.0–2.5 mm long; lobes 5.0–7.1 mm long, 2.1–3.0 mm wide, hairs below sinus absent or sparse; nectary indistinct, 0.2–0.6 mm from corolla base. Filaments 4.2–6.0 mm long from corolla base, 0.3–0.5 mm wide. Anthers 0.4–0.74–1.1 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma crimson, blue, or purple. Ovules 9–18–29 per ovary, ovary colour yellow in maturity. Capsule 6.5–9.5 mm long. FL. Jan–Apr.

DISTRIBUTION (Fig. 57): SOUTH AUCKLAND: Kaimai Range, near Pukepunga. GISBORNE: Huiarau Range (Te Rangaakapua), Urewera (near Lake Waikareiti near Kaipo Lagoon and "Sopps Clearing", Maungapohatu). WELLINGTON: Kaimanawa Mountains, Ruapehu (Hauhangatahi, Mangaturuturu Valley), Ruahine Range.

HABITAT: In and on the margin of montane to subalpine *Nothofagus menziesii* and *Weinmannia sylvicola* forest, under scrub of *Phyllocladus alpinus*, *Halocarpus biformis*, *H. bidwillii*, *Dracophyllum longifolium*, *Myrsine divaricata*, and *Coprosma* spp., with *Lepidosperma australe*, *Carex echinata*, *Chiloglottis cornuta*, *Dicranoloma billardiarei*, *Hypnum cupressiforme*, and *Pyrrhobryum mnioides*; occasionally in tussockland; 750–1350 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: By the shortly pedicellate flowers, by the unbranched caudex, the stout terminal flowering stem and thinner lateral stems which are more or less erect, by the purple corolla veins. *G. chathamica* subsp. *nemorosa* is similar to *G. spenceri* and *G.*

tenuifolia in having purple corolla veins, an unbranched caudex, and a petiolate leaf, but the leaves have an acute-rounded apex, the plants have a stouter terminal flowering stem and thinner lateral flowering stems arising from the basal leaf rosette that are more numerous than in *G. spenceri*. The caudex is more elongated than in *G. spenceri*. It also strongly resembles *G. grisebachii*, from which it differs in having shorter pedicels, a more distinct basal rosette of leaves, and pandurate calyx lobes.

SPECIMENS EXAMINED: *S. Deverill*, Whakapapa, CHR 541819; *L. B. Moore*, Hauhangatahi, CHR 87812; *A. P. Druce*, Kaimanawa Mountains, CHR 402272.

CONSERVATION STATUS: Widespread in the central North Island, but apparently never abundant. The habitat is not threatened.

ETYMOLOGY: *Nemorosa* means "associated with open woodlands".

DISCUSSION: This subspecies was referred to by Druce (1992b) as *Gentiana* "volcanic plateau".

Gentianella concinna (Hook.f.) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 62 (1993).

Basionym: *Gentiana concinna* Hook.f., *Fl. Antarct. 1*: 53, t. 34 (1844). Holotype: *J. D. Hooker*, "Lord Auckland's group, on bleak and exposed faces of mountains", K (photograph seen). Isotype: AK 54670! Label in Hooker's hand says "Very common on hill tops & sides, when grows on the tops attains larger size and purple flowers on their sides fl. white with purple eye, Ld. Aucklands Novr 1841".

≡ *Gentiana cerina* var. *concinna* (Hook.f.) Kirk, *Trans. & Proc. New Zealand Inst.* 27: 339 (1895).

≡ *Chionogentias concinna* (Hook.f.) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

DESCRIPTION: Plants monocarpic, probably biennial, height in flower 27–150 mm. Caudex unbranched. Flowering stems terminal only or terminal and lateral with 1–4 flowering stems per plant, stems 0.7–3.4 mm diameter when dry, lateral flowering stems erect, flowering stem leaves 2–4 pairs per stem, lowest pedicels from halfway up flowering stem. Rosette of leaves distinct or not very distinct from flowering stem leaves; leaves narrowly elliptic, 15–32 mm long, 3.7–8.0 mm wide, margin thickened,

apex rounded, petiole indistinct, c. 10 mm long, 1.0–1.5(–2.5) mm wide at narrowest point. Pedicels 1 or 2 per leaf axil, 4.0–7.0(–11.5) mm long, 0.9–1.1 mm diameter, 0.4–0.6 mm diameter when dry. Flowers (1–)2–22 per plant, 10.5–12 mm long. Calyx 6.0–8.8 mm long; lobes 5.1–8.0 mm long, 2.0–2.3 mm wide at base, plane, apices acute or obtuse, margins minutely serrulate, hairs at calyx-corolla fusion line present, sinus hairs absent. Corolla 8.7–13 mm long, ranging from white to strongly coloured, with purple veins and/or with weak to strong red to purple tinting; tube 2.0–3.0 mm long; lobes 6.7–10.0 mm long, 4.2–6.1 mm wide, hairs below sinus present or absent; nectary 1.2–1.5 mm from corolla base. Filaments 4.1–8.0 mm long from corolla base, 0.55–0.7 mm wide. Anthers 1.2–1.8 mm long. Stigma purple. Ovules 13–40 per ovary. Capsule 7.7–9.0 mm long. FL. Nov–Feb(–Apr).

DISTRIBUTION: Auckland Islands (Auckland Island, Enderby Island, Adams Island).

HABITAT: Coastal turflands, low forest, *Chionochloa antarctica* tussocklands and *Poa littorosa* grasslands, *Marsippospermum gracile* and *Pleurophyllum hookeri* sedgeland on summit fellfields; in low *Metrosideros umbellata*, *Myrsine divaricata*, and *Dracophyllum scoparium* forest, occasionally epiphytic on tree trunks; 0–600 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: Differences from *G. cerina* are listed in Table 11.

SPECIMENS EXAMINED: *C. Meurk*, Tagua Bay, CHR 526412.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Not threatened.

ETYMOLOGY: "Neat, pretty, elegant" (Stearn 1983).

ILLUSTRATION: Hooker (1847, plate 35) has an excellent illustration of the species by J. N. Fitch.

Gentianella corymbifera (Kirk) Holub, *Folia Geobot. Phytotax.* 3: 218 (1968).

Basionym: *Gentiana corymbifera* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 336

(1895). Lectotype (here chosen): *T. Kirk*, St James: Amuri 3000 ft, WELT 4719!
 = *Chionogentias corymbifera* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).
 = *Gentiana pleurogynoides* var. *rigida* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 335
 (1895). Lectotype (here chosen): *Heinrich von Haast*, above Jollies Pass, WELT 47817!
 = *Gentiana bellidifolia* var. *vacillata* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 337
 (1895). Lectotype (here chosen): *J. B. Armstrong*, "Canterbury Plains, 1000 ft", WELT 4716!

DESCRIPTION: Plants biennial, rarely polycarpic, height in flower 60–470 mm. Caudex unbranched, 15–70 mm long. Root branched or unbranched, 1.3–11.3 mm diameter at stem base. Flowering stems terminal only or terminal and lateral with more slender lateral branches from among the rosette leaves, 1–9 per plant, terminal flowering stem 4.2–10.1 mm diameter at base, green or tinted crimson or purple-black, lateral flowering stems erect, internodes 2–4(–6) pairs per stem, lowest pedicels from near base of flowering stem, halfway up flowering stem, or near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves narrowly elliptic to elliptic or ovate, leaf apex acute to rounded, (15–)40–168 mm long, 5.0–31(–33) mm wide, sometimes tinted crimson or purple-black below or on the petiole, usually flat, sometimes V-shaped or channelled at the petiole, petiole 10–40 mm long, (1.5–)3.0–12.0(–18.5) mm wide at leaf base. Flowering stem leaves ovate, apex acute, sessile. Flowers 7–110 per plant, 11–23 mm long, rarely female. Pedicels (1–)2(–3) per leaf axil, (3–)10–40(–50) mm long, (0.64–)0.9–1.5 mm diameter, 0.4–0.8 mm diameter when dry. Calyx 5.2–18 mm long, green or tinted purple-black, crimson or bronze; lobes 2.9–11.3 mm long, 2.7–6.8 mm wide at base, plane, apices acute, margins smooth or minutely serrulate, hairs at sinuses present or absent. Corolla 11.0–21.2 mm long, white, rarely flushed with pink; tube 2.5–12 mm long; lobes 7.5–15.5 mm long, 5.1–10.2 mm wide, hairs below sinus present; nectary 0.7–1.5 mm from corolla base. Filaments 6.4–12.8 mm long from corolla base, 0.8–1.6 mm wide. Anthers (1.5–)1.9–3.2 mm long, anther wall yellow or blue-black, mouth yellow, extrorse, rarely introrse at anthesis. Stigma colourless. Ovules 36–68 per ovary. Capsules 12–19 mm long.

KEY TO SUBSPECIES

- 1 terminal flowering stem 3.0–11.3 mm diameter when fresh, (1.8–)3.7–8.0 mm diameter when dry; leaves 41–168 mm long, 6.5–31 mm wide; calyx lobes 2.7–4.0 mm wide; corolla 14.0–21.1 mm long; filaments 1.1–1.6 mm wide
..... subsp. *corymbifera*
- terminal flowering stem 1.3–7.0 mm diameter when fresh, 0.85–3.7 mm diameter when dry; leaves 15–127 mm long, 5.0–11.3 mm wide; calyx lobes 1.7–2.6(–2.8) mm wide; corolla 11.0–14.6(–15.3) mm long; filaments 0.6–1.2 mm wide
..... subsp. *gracilis*

subspecies *corymbifera*

DESCRIPTION: Plants biennial, rarely polycarpic, 60–350–470 mm in height. Leaves 41–73–168 mm long, 6.5–16.3–31 mm wide; petiole indistinct, 4.0–7.3–18.5 mm wide at leaf base. Flowering stems 1–9 per plant, 3.0–11.3 mm diameter when fresh, (1.8–)3.7–4.7(–8.0) mm diameter when dry. Pedicels (1–)2(–3) per leaf axil, (3–)10–40(–50) mm long, 0.9–1.5 mm diameter. Flowers 7–55–110 per plant, 14–23 mm long. Calyx 6.8–9.4–18 mm long; lobes 3.1–5.9–10 mm long, 2.7–3.0–4.0 mm wide at base. Corolla 14.0–17–21.1 mm long. Filaments 7.2–12.8 mm long, 1.1–1.2–1.6 mm wide. Anthers 1.9–3.2 mm long. FL. late Dec–Jan (montane valleys), Feb–Mar (alpine).

DISTRIBUTION (Fig. 11): NELSON: Anatoki, Lockett, Peel, Arthur, Mt Owen ranges, Ben Nevis, Gordon Range, Glenroy Valley. MARLBOROUGH: Raglan Range, Altamarlock, Wards Peak, Mt Stokes, Benmore, Molesworth Station, Muzzle Creek, Alarm Stream, Puhi Puhi River. CANTERBURY: Island Pass, Clarence Valley, Mt Terako, Hurunui River, Torlesse Range, Porter River, Craigieburn Range, Mt Tripp, Mt Cook (Hooker and Murchison Valleys, Mt Wakefield Spur, Sealy Tarns), Barrier Range (Ohau). OTAGO: Bendhu Wilderness Reserve, Lindis Pass, Crown Range, Ben Lomond. The subspecies is abundant in Nelson and Canterbury. The subspecies appears to be uncommon north of the Awatere Valley and in Otago.

HABITAT: Alpine tall tussocklands of *Chionochloa pallens*, *C. flavescens* and *C. macra* on hillslopes and moraine hummocks; montane, induced *Festuca novae-zelandiae* short

tussockland and tussock grassland on river terraces, colluvial hillslopes and moraine downs, on well drained soils; more rarely in boggy ground with *Schoenus pauciflorus*, *Chionochloa macra*, *Oreobolus pectinatus*, *Carpha alpina*, and *Hebe pauciramosa*; 300–1900 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980); $n = 18$ (Post 1983).

RECOGNITION: The terminal flowering stem is stouter (3.0–11.3 mm diameter) than for any other species. The petiole of the rosette leaves is very wide (4.0–18.5 mm wide), and the rosette leaves are usually large, thick-textured and often have a V-shaped petiole while the lamina is flat. The number of flowers per plant can be large (up to 110 per plant), but this is matched by some other species. The subspecies is almost invariably monocarpic, rare exceptions being found in Westland and Nelson. Gentians that are polycarpic and resemble *G. corymbifera* will usually be either *G. serotina* or *G. montana*. *G. corymbifera* always has a terminal flowering stem whereas the flowering stems are always lateral in *G. serotina*. *G. corymbifera* is not easily distinguished from *G. montana*, especially in Nelson, but a combination of characteristics distinguishes it: a strap-shaped leaf with a wider petiole base than that of *G. montana* leaves, usually a thicker terminal flowering stem base, a denser corymb of flowers, calyx lobes that are triangular with a wide sinus rather than parallel-sided in the lower half and with a wide overlap, a shape very characteristic of *G. montana*. Short but stout plants of *G. corymbifera* can be difficult to distinguish from *G. divisa*. The two are compared in Table 16.

VARIATION: Anthers of Marlborough and North Canterbury populations at lower altitudes are yellow, whereas plants elsewhere have purple anthers with a yellow mouth. In North Canterbury, the subspecies is particularly abundant on the large valley floors of the upper Clarence River valley where the plants lack lateral flowering stems arising from the basal rosette (as shown for Mt Cook plants in Wilson 1978). Alpine populations on the ranges above are more robust plants, which frequently have lateral flowering stems arising from the basal rosette. Subspecies *corymbifera* is abundant south of the Awatere Valley to the Seaward Kaikouras where alpine specimens can be particularly large with leaves 130–168 mm long. At Altamarlock, the corolla lobes have a pink flush, not seen in *G. corymbifera* elsewhere in its range. In Nelson, it is exclusively alpine, and while small plants look similar to North Canterbury specimens,

large plants are distinctive. They are occasionally polycarpic, they may have a long caudex with leaf base scars (in this they resemble *G. montana*), the caudex may be branched and the branches each have terminal flowering stems. When the caudex is unbranched, it is often massively thick and short and the terminal flowering stem is massive with numerous lateral flowering stems originating from bract axils. The Nelson populations may be tending toward polycarpy, possibly via a triennial life cycle where the rosette plants develop a branched caudex before flowering takes place (e.g., *J. A. Hay*, Mt Stokes, CHR 109509). An alternative explanation is that *G. corymbifera* and *G. montana* have hybridised in Nelson.

SPECIMENS EXAMINED: *I. Breitwieser* 2110 & *A. Wilton*, Mt Stokes, CHR 526396; *B. Brown*, Maitland Stream, unvouchered; *D. Glenny* 6281, Upper Clarence Valley, CHR 509799; *D. Glenny* 6408, Mt Cook, CHR 509935; *D. Glenny* 6412, Mt Cook, CHR 509938; *D. Glenny* 6823, Mt Mytton, CHR 530497; *D. Glenny* 6897, No Mans Creek, CHR 530570; *D. Glenny* 6903, Broken River, CHR 559461; *D. Glenny* 7347, Ohau Range, CHR 560149; *D. Glenny* 7351, Ohau Range, CHR 560153; *D. Glenny* 7784, Altimarlock, CHR 525274; *K. Hogan* 2, Altimarlock, CHR 526401; *D. Huson*, Mt Fyffe, CHR 526403; *N. Simpson*, Freehold Creek, CHR 526299; *G. Spearpoint*, Shotover Saddle, CHR 526416.

CONSERVATION STATUS: Widespread and common.

ETYMOLOGY: Having a cluster of flowers.

ILLUSTRATIONS: Mark & Adams (1975, p. 177); Wilson (1978, p. 175) shows a whole plant and leaf.

DISCUSSION: A population of this species from Maitland Stream, Ohau, had female flowers (*B. Brown*, unvouchered), a feature seen more commonly in *G. divisa*. Most specimens are from Canterbury, both from alpine tussocklands and valley bottoms. In Nelson and Marlborough, there are wide gaps in the distribution. The small population on Mt Stokes in the Marlborough Sounds is 63–75 km from the nearest populations known at Wards Peak and Altimarlock, but is distinctive only in having many lateral branches. Two populations on the Richmond Range at Gordon's Knob and Ben Nevis are 70 km north of the nearest populations to the south at the head of the Clarence

Valley. There is also a gap of 65 km from the head of the Clarence Valley to the Nelson populations that have their southern limit at the Marino Mountains. These plants are quite distinctive in the field and are sometimes polycarpic, but analysis of these plants fails to show consistent differences from subsp. *corymbifera* and for this reason, I have not recognised a Nelson subspecies or species. The populations to the north that are of this type are on the Arthur Range, Arthur Tablelands, Garibaldi Ridge, Cobb Valley, Snowden Range, with a northern limit on the Anatoki Range. Two isolated western collections also of this type are from the Trent River (west of the Hurunui River), and Glenroy Valley. The subspecies flowers early on montane river terraces from late December to the end of January, but in alpine areas flowers from February to mid-March.

subspecies *gracilis* Glenny, subsp. nov.

DIAGNOSIS: Ab subspecie *corymbiferae* habitu graciliore, caule florifero terminali angustiore, in statu vivo 1.3–3.1–7.0 mm diametro, in sicco 0.85–3.7 mm diametro, foliis minoribus, angustioribus, 15–127 mm longis, 5.0–11.3 mm latis, lobis calycinis angustioribus 1.7–2.6 (–2.8) mm latis, corolla brevior, 11.0–14.6 (–15.3) mm longa, filamentis angustioribus, 0.8–1.2 mm latis, differt.

HOLOTYPE: *J. Irwin*, Canterbury, South Ashburton Valley, Fagan Downs, 26 Feb 1978, CHR 323378A!

DESCRIPTION: Plants biennial, rarely perennial, 90–210–370 mm in height. Leaves 15–79–127 mm long, 5.0–8.3–11.3 mm wide; petiole 1.5–3.7–5.2 mm wide. Flowering stems 1–3–7 per plant, terminal stem 1.3–3.1–7.0 mm diameter when fresh, 0.85–3.7 mm diameter when dry. Pedicels 1–2 per axil, 10–30 mm long, 0.64–1.1 mm diameter. Flowers (5–)10–27–98 per plant, 11.0–15.5 mm long at anthesis. Calyx 5.2–6.5–8.5 mm long; lobes 2.9–4.4 mm long, 1.7–2.1–2.6 (–2.8) mm wide. Corolla 11.0–13.4–14.6 (–15.3) mm long, white, rarely with veins violet. Filaments 6.4–9.2 mm long, (0.6–)0.8–0.92–1.2 (–1.4) mm wide. Anthers (1.5–)2.0–2.3–2.7 mm long. FL. late Dec–Mar.

DISTRIBUTION (Fig. 11): CANTERBURY: Waimakariri River (*R. Mason*, CHR 51448), Castle Hill Basin, Ashburton Lakes, Mt Peel, Hunter Hills, Tasman Valley, Sebastopol

Tarns, Lake Pukaki, Ohau Valley, Ahuriri Valley, Tekapo. OTAGO: Luggate, Lake Hawea, Coronet Peak, Skippers Creek, Arrow River, Queenstown Hill. SOUTHLAND: Eyre Mountains, Jane Peak.

HABITAT: Eastern South Island montane basins, on moraine downs, outwash terraces, and lower hillslopes, in *Festuca novae-zelandiae*, *Anthoxanthum odoratum*, and *Agrostis capillaris* tussocklands and grasslands. In Otago, it formerly occupied outwash surfaces (e.g., at Hawea Flats), but is also on hillslopes and rock outcrops near creeks (e.g., at Skippers Creek) where it associates with herbaceous species such as *Dolichoglottis lyallii*, *Ourisia caespitosa*, *Anaphalioides bellidioides*, and *Hypericum perforatum*.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: A slender form of *G. corymbifera*, which has narrower leaves (<11.3 mm wide, cf. up to 31 mm wide in subsp. *corymbifera*), smaller flowers (corolla up to 15 mm, cf. up to 21 mm in subsp. *corymbifera*). The two subspecies overlap in the range of most size attributes but subsp. *gracilis* is on average recognisably smaller, particularly when a whole population is seen in the field. In South Canterbury, subsp. *gracilis* occurs in the intermontane basins at lower altitude on moraines and outwash surfaces, while subsp. *corymbifera* occurs in the alpine zone.

VARIATION: Varies considerably in stature (e.g., from 90 to 370 mm tall, with terminal flowering stems 1.3–7.0 mm diameter) because its bienniality forces small plants to flower regardless of size. Ashburton Lakes specimens have a membranous calyx margin not possessed by other populations. A population in Skippers Creek is distinctive in having yellow anthers.

SPECIMENS EXAMINED: *D. Glenny* 6401, Skippers Creek, CHR 509926; *D. Glenny* 7333, Fagan Downs, CHR 560136; *D. Glenny* 7335, Cameron Fan, CHR 560138; *D. Glenny* 7354, Sawyers Creek, CHR 560154; *P.N. Johnson* 1423, Glenmore Tarns, CHR 518390; *N. Simpson*, Ohau Range, CHR 526299.

CONSERVATION STATUS: Common in areas where found.

ETYMOLOGY: *Gracilis* means "slender", referring to the generally narrower leaves and

flowering stems giving the plant a less robust appearance than the type subspecies.

ILLUSTRATIONS: Moore & Irwin (1978, p. 147, fig. 1), the plant illustrated is the type; Wilson (1978, p.174, fig. 308); Wilson (1996, p. 222), fig. 321, as "(a) narrow-leaved forms: montane river flats, feet of spurs" showing a single leaf.

DISCUSSION: Specimens of this subspecies at CHR were formerly unidentified (13 specimens), identified as *G. serotina* (5 specimens), *G. corymbifera* (2 specimens), as *Gentiana* "Skippers" (6 specimens), or *G. patula* (2 specimens). *G. serotina* never has terminal flowering stems and flowers later than *G. corymbifera*, which in the montane basins peaks in its flowering in late January. A. P. Druce considered *G. "Skippers"* to be close to *G. serotina*, but all specimens determined as *G. "Skippers"* have a terminal flowering stem.

The two subspecies of *G. corymbifera* are parapatric in South Canterbury, in that only altitude separates them at localities such as Freehold Creek in the Ohau Range where subsp. *gracilis* occurs on moraine downs at 540–700 m, while subsp. *corymbifera* occurs directly above and is abundant at 1400 m and occurs occasionally down to 1100 m.

There may be difficulty in distinguishing the two at intermediate altitudes. The northern limit of subspecies *gracilis* is at the limestone area of Castle Hill Basin (*G. Brownlie*, CHR 344906). The subspecies does not become abundant until further south, on the moraine downs of the Ashburton River.

Gentianella decumbens Glenny, sp. nov.

DIAGNOSIS:- *Gentianellae bellidifoliae* affinis, sed habitu maiore e rosula lata ramis prostratis radiantibus praedita composito, 170–400 mm diametro, pluribus caulis floriferi (4–22) ad peripheriam plantae, foliis caulinis imbricatis, numerosis, in paribus (4–)6–9, filamentis angustioribus quam eis *G. bellidifoliae*, 0.9–1.1 mm latis (non 0.8–2.0 mm latis), nectario 1.6–2.3 mm ex base corollae, statione in summis montanis et lineis cristarum in agris planis glareosis plerumque saxorum arenaceorum vegetatione sparsa praeditis differt.

HOLOTYPE: *D. Glenny* 7437, Peel Range, 1490 m, 7 March 1998, CHR 560059 (Fig. 28).

DESCRIPTION: Plants polycarpic, height in flower 80–140(–200) mm, plants 170–400

mm diameter. Caudex branched, 40–220 mm long, stolons absent. Root 3.1–6.2 mm diameter at stem base. Flowering stems (1–)4–12–22(–27) per plant, lateral only, decumbent, green or crimson, largest stems 1.4–2.5 mm diameter at base, 1.4–2.0 mm diameter when dry; stem leaves (4–)6–9 pairs per stem with internodes often short, the last pair often at the calyx base, sometimes sheathing the stem; lowest pedicels from near apex of flowering stem. Leaf rosette of leaves absent to distinct from flowering stem leaves. Basal leaves elliptic, leaf apex acute to rounded, (16–)20–29–44(–48) mm long, 5.3–8–10.4 mm wide, green without tinting, often turning yellow with age, V-shaped in section or channelled, recurved toward the leaf apex; petiole moderately distinct, 12–30 mm long, 2.2–2.7–3.6 mm wide at leaf base. Pedicels 1 per leaf axil, 0–19 mm long, 1.1–1.7 mm diameter, 1.0–1.4 mm diameter when dry. Flowers (3–)22–72 per plant, 16–20 mm long, rarely female. Calyx 8.0–9.5–12.0 mm long, green, hairs at calyx–corolla fusion line present; lobes 5.2–6.5–8.4 mm long, (2.6–)2.9–3.2–5.1 mm wide at base, apices acute, margins recurved, smooth to minutely serrulate, sinus hairs abundant. Corolla 14.0–16.2–19.8 mm long, white; tube 2.8–6.3 mm long; lobes 10.5–13.4 mm long, 7.3–11.1 mm wide, hairs below sinus abundant; nectary (1.0–)1.1–1.6–1.9(–2.3) mm from corolla base. Filaments 9.0–12.5 mm long from corolla base, 0.9–1.0–1.1 mm wide. Anthers 2.3–2.6–2.7 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules 26–37–56(–60) per ovary, ovary yellow in maturity. Capsules 18–29 mm long. FL. Jan–early Mar.

DISTRIBUTION (Fig. 58): NELSON: Lead Hills, Haupiri Range, Anatoki Range, Devil Range, Snowdon Range, Mt Domett, Lockett Range (Iron Hill, Mt Benson, Lake Sylvester), Peel Range, Lodestone, Arthur Range (Loveridge Peak, Mt Star), Matiri Plateau, and Haystack.

HABITAT: Usually on bare or nearly bare fellfield or rock pavement on ridges, growing in stony soils, on sandstone, schist, granite, on calcareous sandstone at Matiri Plateau, and never on marble. Also in sparse tussocklands of *Chionochloa pallens* and/or *C. australis*, and in shrublands; 1030–1700 m.

CHROMOSOME NUMBER: $n = 18$ and c. 18 (Post 1983 as *Gentiana bellidifolia*).

RECOGNITION: A large species when fully grown, with many branches spreading radially

from the taproot, so that the plant becomes a rather flat radiating mat of c. 250–400 mm diameter. Flowering stems are mostly found on the perimeter of the plant, along with the dead previous season's flowering stems. Leaves are channelled and the flowers are large as in *G. bellidifolia*, but plants of *G. bellidifolia* s. s. never attain the size of *G. decumbens*. The flowering stem leaves are more numerous, and often sheath the stem. There is often a pair of flowering stem leaves that are joined at the base of the calyx and these can appear to be an extra pair of calyx lobes. *G. decumbens* has the nectary further from the corolla base than *G. bellidifolia* (on average 1.9 mm from the base, compared to an average of 0.8 mm from the base in *G. bellidifolia*) and has relatively narrow filaments, averaging only 1.0 mm at the widest point, while *G. bellidifolia* has filaments that average 1.2 mm wide and are up to 2.0 mm wide.

VARIATION: Relatively uniform throughout its range. Plants at the Matiri Plateau grow out of rock pavement crevices and cliff crevices and do not have the symmetrically spreading form of most examples of *G. decumbens*, but share their floral and leaf dimensions and multiple branching.

SPECIMENS EXAMINED: *I. Breitwieser* 2005 & *R. Vogt*, Round Lake, CHR 516222; *A. P. Druce*, Mt Lodestone, CHR 277645; *A. P. Druce*, head of Cobb Valley, CHR 310378; *A. P. Druce*, Matiri Plateau, CHR 355165; *D. Glenney* 8103b, Lead Hills, CHR 565236; *A. F. Mark*, Lake Sylvester, OTA 025890 & 025054; *R. Mason*, Anatoki Range, CHR 34919.

CONSERVATION STATUS: Restricted in distribution and not common, but not threatened at present.

ETYMOLOGY: From *A. P. Druce*'s tag name "decumbent", referring to its branches, which lie along the ground and rise at the terminal rosettes, with erect flowering stems.

ILLUSTRATIONS: Metcalf (1996, #35 and front cover) as *Gentiana bellidifolia* var. *australis*; Mark & Adams (1973, plate 76 upper right) as "Cobb Valley gentian". OTA 26054 appears to be the specimen illustrated. The habitat notes say "poorly drained sites in snow tussock-herbfield" but *G. decumbens* always grows in well drained sites.

DISCUSSION: In the field, this is a very distinct entity, not easily mistaken for the smaller

G. bellidifolia. However, it differs little from *G. bellidifolia* in its leaf and flower dimensions. Both occur on the Peel and Lockett ranges, but in different habitats: *G. bellidifolia* in moist soils by lakes and in flushes, *G. decumbens* mainly on the ridges, at sites separated from *G. bellidifolia* by c. 500 m of altitude.

Gentianella divisa (Kirk) Glenney, comb. nov.

Basionym: *Gentiana bellidifolia* var. *divisa* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 337 (1895). Lectotype (here chosen): *T. H. Potts*, Ashburton Mountains, WELT 4714!

flowering plant on left of sheet. Notes say: "Calyx divided nearly to the base linear oblong obtuse. Corolla divided nearly to base, lobe rounded at the apex, spreading."

≡ *Gentiana divisa* (Kirk) Cheeseman, *Man. New Zealand fl.* 453 (1906).

≡ *Gentianella bellidifolia* var. *divisa* (Kirk) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

≡ *Chionogentias divisa* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

DESCRIPTION: Plants monocarpic, biennial, possibly triennial, height in flower (40–)60–150(–200) mm. Caudex unbranched, c. 20 mm long. Root 2–6 mm diameter at stem base. Flowering stem terminal, 1.7–5.0 mm diameter at base, 1.4–4.0 mm diameter when dry, stem colour green, tinted slightly purple-black, or bronze, lateral branches of the flowering stem erect to decumbent, flowering stem leaves 0–4 pairs per stem, lowest pedicels from near base of flowering stem to near apex of flowering stem. Rosette of leaves absent to distinct from flowering stem leaves; leaves elliptic or orbicular or obovate or narrowly obovate, 16–65 mm long, 7.5–21 mm wide, green, usually flat, sometimes V-shaped in section or channelled, slightly recurved or not; petiole indistinct, c. 13 mm long, 2.8–8.0 mm wide at leaf base; leaf apex rounded. Flowering stem leaves narrowly ovate. Pedicels 1 or 2 per leaf axil, 7–50 mm long, 1.0–1.9 mm diameter, 0.5–1.2 mm diameter when dry. Flowers 11–60 per plant, 15–20 mm long, often female. Calyx 8.5–11.0 mm long, green or bronze, or green tinted purple-black at lobe apices, hairs at calyx-corolla fusion line absent; lobes 5.0–9.0 mm long, 2.0–5.0 mm wide at base, plane but surface often rugose, apices acute, margins smooth or minutely serrulate, sinus hairs sparse to abundant. Corolla 13.5–18.6 mm long, white; tube 3.0–5.6 mm long; lobes 10.2–14.5 mm long, 5.2–9.5 mm wide, hairs below sinus present; nectary 0.6–1.9 mm from corolla base. Filaments 8.5–13.4 mm long from corolla base, 0.9–2.4 mm wide. Anthers 1.9–2.8 mm long, anther wall blue-black, mouth yellow or orange-red, extrorse at anthesis. Stigma colourless, purple, crimson, or blue. Ovules

29–56(–76) per ovary, ovary yellow or purple-black in maturity. Capsule 15–17 mm long. FL. Jan–Mar.

DISTRIBUTION (Fig. 59): CANTERBURY: Upper Hurunui (Mt Studleigh), Torlesse Range (Castle Hill), Craigieburn Range (Hamilton Peak), Upper Rangitata valleys, Mt Cook. WESTLAND: Marks Flat, Karangarua River, Copland Range Mt Fox, Alex Knob, Barlow River, Lord Range, Wilberg Range, Whitcombe Valley, Waitaha Valley, Hitchin Range, Griffin Range. OTAGO: Cascade Valley, Olivine Range, Richardson Mountains, Beans Burn, Wilkin Valley, Hunter River, Mt Earnslaw, Matukituki Valley, Remarkables, Old Man Range, Dunstan Range, Pisa Range, Mt Cardrona, Rock and Pillar Range. SOUTHLAND: Mid Dome, Darra Mountains, Lake Wapiti, Mt George, Centre Pass, Dusky Sound, Doubtful Sound. More abundant in the southern part of the range. In Mid and North Canterbury known from only a few sites.

HABITAT: In Canterbury on alpine ridge-top fellfields and low-angled scree, with *Haastia sinclairii*, *Koeleria cheesemanii*, *Colobanthus acicularis*, 900–2300 m; in Central Otago in alpine matfields, cushionfields, and herbfields, with *Dracophyllum muscoides*, *Kelleria dieffenbachii*, *Euchiton mackayii*, *Carex gaudichaudiana*, *Polytrichum commune*, 1000–1830 m; in Westland, West Otago, and Fiordland in alpine tussockland of *Chionochloa pallens* and *C. teretifolia* and at the base of or on bluffs, with *Dolichoglottis lyallii*, *Geum parviflorum*, *Anaphalioides bellidioides*, *Celmisia walkeri*, *C. petriei*, *Aciphylla similis*, and *Anisotome haastii*; 800–1530 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980, Dawson & Beuzenberg 2000); $n = 18$ (Post 1983).

RECOGNITION: By the unbranched caudex, the single taproot, the leaves flat, more or less orbicular with obtuse apices on a wide petiole (4 mm wide); the central flowering stem equal in size to the many branches giving a dense, even surface of flowers. The calyx lobes are wide, project along the lobe fusion lines or overlap each other more than usual, are rugose on their outer surfaces, and often have six calyx lobes. *G. filipes* shares these features, but is smaller in all its parts. *G. divisa* can be difficult to tell from *G. corymbifera* at times, especially in Otago. *G. divisa* is usually shorter (Table 16), and with a much denser branching structure so that the main stem is difficult to see inside the mass of flowers. *G. divisa* usually has a more slender main flowering stem, but the two

species overlap in this dimension. *G. divisa* is often female, whereas *G. corymbifera* is rarely so. The calyx of *G. divisa* commonly has the "abnormal" appearance described above while *G. corymbifera* generally lacks this abnormal appearance, although six calyx lobes are occasionally seen.

VARIATION: Fiordland and Westland plants are less compact but are smaller than Central Otago and Canterbury plants, have smaller leaves, fewer flowers, have more flowering stems branching from the base of the rosette, and are found in well vegetated alpine habitats. In other words, they look more like small forms of *G. corymbifera*, but that species is not in the same high rainfall habitats and is absent from Fiordland, South and Central Westland. In Canterbury the species is found mainly in very sparsely vegetated greywacke fellfield on the main ridges, and the plants are often large with stout taproots, many flowers, and a single stout flowering stem that is much branched. Otago plants are intermediate between Southland and Canterbury forms. When only the extremes of the variation are seen, it is difficult to accept that one species is involved, but in Otago intermediates between the extremes are seen. *G. "Skeleton"* of A. P. Druce, from Central Otago, is not accepted as distinct, as it falls within the variation seen within *G. divisa* in all respects.

SPECIMENS EXAMINED: *B. Brown*, Gillespie Pass, CHR 526443; *D. Glenny* 6850, Gertrude Saddle, CHR 530527; *D. Glenny* 6872, Harris Saddle, CHR 530548; *D. Glenny* 7315, Polnoon Burn, CHR 559587; *D. Glenny* 7476 & 7458, Lake Wapiti, CHR 560103, 560085; *D. Glenny* 7668, Pisa Range, CHR 529424; *D. Glenny* 7701, Rock and Pillar Range, CHR 529454; *G. Spearpoint*, Hitchin Range, CHR 518969; *G. Spearpoint*, Shotover Saddle, CHR 526417; *K. Wardle*, Earnslaw Burn, CHR 526419.

CONSERVATION STATUS: Common in Otago and South Canterbury, but only at a few sites in North Canterbury on the Craigieburn and Torlesse ranges.

ETYMOLOGY: *Divisa* means "divided". Wilson (1978) suggests this refers to the many flowering-stem branches.

ILLUSTRATIONS: Salmon (1968, p. 241, plate 329); Wilson (1978, p.175, fig. 309).

Gentianella filipes (Cheeseman) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 62 (1993).

Basionym: *Gentiana filipes* Cheeseman, *Trans. & Proc. New Zealand Inst.* 28: 536 (1896). Lectotype (here chosen): *T. F. C.[heeseman]*, "Mt Arthur, Nelson, alt. 5000 ft. Jan 1886", AK 7160! plant at centre-right, within pencilled box, annotated "Type selected (L. M. Cranwell) July 8, 1942".

≡ *Chionogentias filipes* (Cheeseman) L.G.Adams, *Austral. Syst. Bot.* 8: 976 (1995).

DESCRIPTION: Plants monocarpic, annual, height in flower 20–140 mm. Caudex unbranched, 25–35 mm long. Root 0.5–0.9 mm diameter at stem base. Flowering stems terminal and lateral, 2–8 per plant, central flowering stem 0.9–1.9 mm diameter at base, 0.3–1.0 mm diameter when dried; stem colour green, tinted crimson or purple-black, lateral flowering stems erect to decumbent, flowering stem leaves 1–5 pairs per stem, lowest pedicels from near base of flowering stem to near apex of flowering stem. Rosette of leaves absent from flowering plants, basal leaves narrowly elliptic or elliptic or ovate, 9–20 mm long, 2.6–6.4 mm wide, green, flat, not recurved, apex acute or rounded; petiole distinct or indistinct, 3.5–8.8 mm long, 1.0–2.6 mm wide at leaf base. Flowering stem leaves elliptic to ovate, apices rounded or acute. Pedicels 1 per leaf axil, 4.5–32 mm long, 0.7–1.8 mm diameter, 0.5–0.7 mm diameter when dry. Flowers 1–30(–81) per plant, 8.2–13 mm long, sometimes female. Calyx 6.0–8.5 mm long, green tinted purple-black, at lower lobe margins, hairs at calyx-corolla fusion line absent or present; lobes 2.6–5.0 mm long, 2.2–5.2 mm wide at base, strongly ridged between the lobes, plane or recurved, margins smooth, apices acute, sinus hairs abundant. Corolla 7.6–12 mm long, white, sometimes tinted purple at corolla tips; tube 2.6–4.6 mm long; lobes 4.5–8.3 mm long, 3.3–5.9 mm wide, hairs below sinus absent or present; nectary 0.4–1.1 mm from corolla base. Filaments 4.3–7.8 mm long from corolla base, 0.6–0.9 mm wide. Anthers 0.8–1.4 mm long, anther wall blue-black, occasionally pale blue, mouth yellow, extrorse or horizontal at anthesis. Stigma colourless. Ovules 11–32 per ovary. Capsule 8–9 mm long. FL. Jan–Apr.

DISTRIBUTION (Fig. 60): NELSON: Cobb Valley, Devil Range, Garibaldi Range, Arthur Range, Owen Range, Patriarch, Matiri Range, Glenroy Valley.

HABITAT: Alpine grasslands dominated by *Poa colensoi*, marble scree and talus, rock crevices, peat bog, gravel riverbed, with *Chionochloa pallens*, *Aciphylla colensoi*,

Celmisia traversii, *Ranunculus insignis*, *Rytidosperma setifolium*, *Anisotome aromatica*, *Anaphalioides bellidioides*, *Anthoxanthum odoratum*; 915–1615 m. Mainly found in areas of marble, usually in shallow soils over bedrock, but not exclusively so.

CHROMOSOME NUMBER: $n = 18$ (Post 1983).

RECOGNITION: By its annual life cycle as indicated by there being no rosette plants present at flowering time, by the variation in the number of flowers per plant, and by the very small tap root. The plants grow gregariously. For their size (<100 mm tall), the flowers are abundant. There is no basal leaf rosette in flowering plants. The base of each calyx lobe is recurved and there is a prominent ridge on the calyx below each sinus. The calyx lobes are short and wide (sometimes wider than long), and very unequal (the smallest $\times 0.5$ – 0.6 the largest). The flowers are small (12–13 mm long) as are the basal leaves (to 20 mm long). The similarity of the calyx to that of *G. divisa* suggests the two are sibling species. The two are widely allopatric.

VARIATION: A distinct species in which all variation appears to be habitat induced.

SPECIMENS EXAMINED: *D. Glenny* 6816, Mt Mytton, CHR 530490; *D. Glenny* 7374, Mt Owen, CHR 565002; *D. Glenny* 7441, Horseshoe Basin, CHR 560069; *A. Wilton & K. Ford* 67/98 Garibaldi Ridge, CHR 513665.

CONSERVATION STATUS: Common within its distributional and habitat range.

ETYMOLOGY: *Filipes* means "slender foot", referring to the slight root, a characteristic of small annual species.

ILLUSTRATION: Fig. 61.

Gentianella gibbsii (Petrie) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

Basionym: *Gentiana gibbsii* Petrie, *Trans. & Proc. New Zealand Inst.* 49: 52 (1917).

Lectotype (here chosen): *F. G. Gibbs*, "Stewart Island", ex herb. Petrie with note: "L.

Cockayne to me ex *F. G. Gibbs*.", WELT 4709! Isotype: "Boggy ground, Mt Anglem, Stewart Island, *F. G. Gibbs*, Jan 1907" WELT 47783! ex. herb. L. Cockayne.

≡ *Chionogentias gibbsii* (Petrie) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

DESCRIPTION: Plants monocarpic, biennial, height in flower 60–200 mm. Caudex unbranched, 10–25 mm long. Root c. 0.9 mm diameter at stem base. Flowering stems terminal only or terminal and lateral, 1–19 per plant, largest flowering stem 1.0–1.6 mm diameter at base, 0.8–1.6 mm diameter when dry, stem colour bronze, lateral flowering stems erect, flowering stem leaves 2–4 pairs per stem, lowest pedicels from halfway up flowering stem or near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves elliptic, leaf apex acute, 13–22 mm long, 3.6–7.0 mm wide, green, channelled, not recurved, petiole 7.3–14.5 mm long. Petiole 1.0–1.2 mm wide at leaf base. Flowering stem leaves narrowly elliptic. Pedicels 1 per leaf axil, 4.5–60 mm long, 0.8–1.1 mm diameter, 0.8–1.2 mm diameter when dry. Flowers 1–28 per plant, 12.5–14.9 mm long. Calyx 9.5–14.7 mm long, bronze-green, hairs at calyx-corolla fusion line present; lobes 8.5–11.8 mm long, 1.7–2.0 mm wide at base, plane, apices acute, margins smooth, sinus hairs sparse. Corolla 11.7–15.3 mm long, white; tube 3.0–3.5 mm long; lobes 8.8–12 mm long, 5.0–6.5 mm wide, apices acute and slightly serrated, hairs below sinus absent or present; nectary 1.7–2.0 mm from corolla base. Filaments 6.5–8.6 mm long from corolla base, 0.5–1.1 mm wide. Anthers 1.1–1.9 mm long, anther wall blue-black, mouth yellow, introrse at anthesis; pollen yellow. Stigma colourless. Ovules 36–49 per ovary. Capsule 15.3–27 mm long. FL. Jan–Mar.

DISTRIBUTION: STEWART ISLAND: Mt Anglem, Little Mt Anglem.

HABITAT: Alpine, commonly growing through hummocks of *Dracophyllum politum*, otherwise on soil under *Olearia colensoi* scrub and in the open in *Dracophyllum* shrublands and *Chionochloa pungens* tussockland; 860–980 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: By the very long, narrowly triangular calyx lobes. On Stewart Island *G. gibbsii* occurs with *G. lineata* but is taller (plants 60–200 mm high, not 70–100 mm high) and biennial, and has a bronze colour whereas *G. lineata* is polycarpic, has a branched caudex, and is dark green with purple tinting.

SPECIMENS EXAMINED: *D. Glenny* 6346, Mt Anglem, CHR 509867.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001).
Common on Mt Anglem, a Nature Reserve.

ETYMOLOGY: Named for F. G. Gibbs (1866–1953), progressive educator and headmaster of Nelson (Tunnickliff, 2002).

ILLUSTRATION: Wilson (1982, p. 248).

DISCUSSION: *G. gibbsii* and *G. lineata* share an inbreeding syndrome with the anthers introrse at anthesis, presumably an adaptation to a situation in which there are few pollinators. *G. gibbsii* resembles large Southland plants of *G. grisebachii* in its bronze colour, its size and erect branches and may have its origin in such South Island populations.

Gentianella grisebachii (Hook.f.) T.N.Ho in Ho & Liu, *Bull. Brit. Mus. (Nat. Hist., Bot.* 23: 63 (1993).

Basionym: *Gentiana grisebachii* Hook.f., *Icones Plantarum* t. 636 (1844). Holotype: J. C. Bidwill, "on the downs between Rotoaira and the base of Tongariro", K (photograph seen). The type matches the plate in *Icones Plantarum*.

≡ *Gentiana montana* f. *grisebachii* (Hook.f.) Kirk, *Trans. & Proc. New Zealand Inst.* 27: 334 (1895).

≡ *Oreophylax grisebachii* (Hook.f.) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

≡ *Chionogentias grisebachii* (Hook.f.) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

= *Gentiana novae-zelandiae* J.B.Armstrong, *Trans. & Proc. New Zealand Inst.* 4: 290 (1872). Holotype: J. B. Armstrong, Rangitata River, Mt Potts, CHR! Specimen on top left of sheet so marked. Label notes: "flowering stems black when fresh, flowers yellow", CHR! Isotype: J. B. Armstrong, Southern Alps. "Type of *G. novae-zelandiae*" written in Cheeseman's handwriting, AK 7179!

≡ *Gentiana montana* f. *novae-zelandiae* (J.B.Armstrong) Kirk, *Trans. & Proc. New Zealand Inst.* 27: 334 (1895).

≡ *Gentiana grisebachii* var. *novae-zelandiae* (J.B.Armstrong) Cheeseman, *Man. New Zealand fl. Ed.* 2 727 (1925).

= *Gentiana matthewsii* Petrie, *Trans. & Proc. New Zealand Inst.* 44: 138 (1912).

Lectotype (here chosen): *D. P[etrie]*, Lake Harris, Routeburn: Lake Wakatipu, 27:2:1911, with the note "Perhaps only a var. of *G. Grisebachii* Hk. f.", WELT 4710!

plant on right of sheet. Isolectotype: 79965!

≡ *Gentiana grisebachii* var. *matthewsii* (Petrie) Cheeseman, *Man. New Zealand fl. Ed. 2* 727 (1925).

≡ *Gentianella matthewsii* (Petrie) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 63 (1993).

≡ *Chionogentias matthewsii* (Petrie) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

DESCRIPTION: Plants monocarpic, biennial, height in flower 40–290 mm. Caudex unbranched, 7–15 mm long. Root 1.4–4.0 mm diameter at stem base. Flowering stems terminal and lateral or lateral only, 2–8 per plant, largest flowering stem 0.6–2.7 mm diameter at base, 0.8–1.5(–3.1) mm diameter when dry, stem green, or tinted crimson-orange, or purple-black, lateral flowering stems erect or decumbent, flowering stem leaves 3–6 pairs per stem, lowest pedicels from near base of flowering stem to near apex of flowering stem. Rosette of leaves absent from flowering plants, leaves narrowly elliptic or elliptic or ovate, 9.1–65 mm long, 2.3–10.5(–16) mm wide, green or tinted purple-black, flat or V-shaped in section, not recurved; apex acute or rounded; petiole distinct, 11–18 mm long, 0.7–2.3(–3.6) mm wide at leaf base. Flowering stem leaves elliptic, ovate to narrowly ovate. Flowers 3–49 per plant, 6.7–12.5(–20) mm long. Pedicels 1 per leaf axil, 10–80 mm long (elongating after flowering to 17–85 mm), 0.5–1.4 mm diameter, 0.4–0.9 mm diameter when dry. Calyx 5.5–11.6 mm long, green, tinted purple-black at the apices, hairs at calyx-corolla fusion line present; lobes 4.2–7.8 mm long, 0.9–2.6 mm wide at base, plane, apices narrowly acute, margins smooth, sinus hairs absent or sparse. Corolla 6.4–16 mm long, white, occasionally a purple-grey tinting on the corolla lobes, with veins uncoloured, purple or purple-grey; tube 1.5–3.8 mm long; lobes 4.9–12.5 mm long, 2.1–8.6 mm wide, hairs below sinus absent or present; nectary 0.4–1.2 mm from corolla base. Filaments 3.6–8.6 mm long from corolla base, 0.3–1.1 mm wide. Anthers 0.5–3.4 mm long, anther wall blue-black, rarely pink, mouth yellow, pale orange or orange-red, extrorse, occasionally horizontal at anthesis; pollen yellow or pale orange. Stigma colourless. Ovules 23–72 per ovary. Capsule 7.2–20 mm long. FL. Jan–Mar.

DISTRIBUTION (Fig. 21): GISBORNE: Maungapohatu, Mt Raukumara. TARANAKI: Ahimanawa Swamp. WELLINGTON: Rotoaira, Ruapehu, Kaimanawa Mountains, Rangitikei River, Reporoa Bog, Mokai Patea Range, Whana Huia Range, Oroua River, Tararua Range (Mt Kaiparoro, West Peak, Te Matawai, Mt Waiopahu, Oriwa Lake,

Tarn Ridge, Holdsworth, Kapakapanui, Maymorn), Rimutaka Range. NELSON: Marino Mountains, Spenser Mountains, Upper D'Urville River, Matiri Range, Lewis Pass. MARLBOROUGH: Chalk Range, Tarndale, Acheron River. CANTERBURY: Doubtful River, Hope River, Esk River, Cass, Coleridge Lakes, Heron Basin, Hooker Valley, Tekapo, Two Thumbs Range, Banks Peninsula (Devils Gap), Lake Ellesmere (*T. Kirk*, Lake Road, 1884). WESTLAND: West of Lake Sweeney, Marks Flat. OTAGO: Hunter Valley, Reese Valley, Nevis Valley, Old Man Range (Campbell Creek), Humboldt Mountains (Lake Harris), Wilkin Valley, Lammerlaw Range, Rock and Pillar Range, Swampy Hill, Maungatua, Otago Peninsula. SOUTHLAND: Garvie Mountains, Blue Mountains, Mavora Lakes, Weydon Burn, Otaitai Bush, Awarua Bay, Clinton, Waitutu, Twinlaw Peak, Dipton, Oreti Beach, Colac Bay, Longwood Range, West Dome, Fiordland (Gertrude Valley, Clinton River, Lake Marion, Caswell Sound, Wet Jacket Arm, Dusky Sound, Mt Soaker, Mt George, Wilmot Pass). STEWART ISLAND: Rakiwha Valley, Ringaringa, Ruggedy Flats.

HABITAT: Mesotrophic to oligotrophic wetlands (marshes, swamps, flushes, and bogs). Damp tussockland of *Chionochloa rubra*, *C. pallens*, *C. crassiuscula*, *C. rigida*, often with sparse shrubs of *Leptospermum scoparium*, *Hebe pauciramosa*, *H. cockayneana*, *Ozothamnus leptophyllus*; swamps and lake margins in rushlands, sedgeland and herbfields of *Juncus effusus*, *Agrostis tenuis*, *Gonocarpus micranthus*, *Centella uniflora*, *Plantago triandra*, *Hypsela rivalis*, *Polytrichum commune*, *Schoenus maschalinus*, *Nertera depressa*, *Schoenus pauciflorus*, *Carex gaudichaudiana*, *Cyperus alpinus*, *Bulbinella*, *Oreomyrrhis*, *Oreobolus pectinatus*, *Celmisia glandulosa*, *Dolichoglottis lyallii*, *Astelia linearis*, *Psychrophila novae-zelandiae*, *Drosera arcturi*, and *Sphagnum cristatum*; kettlehole tarns in short turflands, grasslands on river terraces and hillslope pasture, with *Anthoxanthum odoratum*, *Agrostis tenuis*, *Coprosma petriei*, *Gonocarpus micranthus*, *Leucopogon fraseri*, *Pratia angulata*; in bogs of *Empodisma minus*, *Eleocharis gracilis*, *Centrolepis ciliata*, *Juncus pusillus*, *Celmisia gracilentia*, *Gaultheria macrostigma*, *Sphagnum cristatum*; rarely on papa cliffs in seepage zones, with *Machaerina sinclairii*, *Blechnum novae-zelandiae*, *Brachyglottis rufiglandulosus*; in the Ruahine and Rimutaka ranges in well drained sites under scrub of *Leptospermum scoparium* and in forest openings, e.g., in *Nothofagus menziesii* and *Weinmannia racemosa* forest on ridgetops, with *Dicranoloma billardiarii*, *Lycopodium volubile*, and *Rytidosperma nigricans*; 0–1524 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980, Dawson & Beuzenberg 2000); $n = 18$

(Post 1983).

RECOGNITION: By its usual preference for wet mesotrophic habitats, its large number of dark purple or bronze scapes, its elongated pedicels after flowering, its narrowly triangular calyx lobes, sometimes by its small flowers that hardly open.

VARIATION: This species varies more than any other *Gentianella* species in New Zealand. The robust part of this variation was expressed in the recognition of *G. matthewsii*. Large plants that fit the concept of *G. matthewsii* are present throughout the distributional range of *G. grisebachii*, but are most common in Southland and the lower North Island. Some of this variation in size is caused by habitat, large plants being found in taller vegetation of fertile wetlands, while the smallest plants are found in short turflands in seasonally dry kettleholes or on river terraces. Most of this variation between such sites is phenotypic, but there is also a genetic component that seems to be very fine grained (sometimes on a scale of tens of metres), possibly because of selfing and short pollinator ranges. A division of this species aggregate into two species or subspecies on size is impractical since all size intermediates can be found.

Colour in the corolla of *G. grisebachii* varies from being absent, to purple or violet in the veins, to a tinting on the corolla lobes. Similarly, the stigma is usually colourless, but is occasionally purple, violet or blue. In small plants, the stems and calyces are usually tinted purple-black, while in large plants in Southland a bronze or crimson colour or a colour intermediate between these two is most common, although large plants can be tinted purple-black (e.g., at the type locality of *G. matthewsii* below Lake Harris).

SPECIMENS EXAMINED: *B. Brown*, Siberia Stream, CHR 526442; *B. Brown*, Forgotten River, CHR 510004; *S. Courtney*, Eric Stream, CHR 526399; *D. Glenny* 6380, Blue Lake, CHR 509906; *D. Glenny* 6385, Garvie Mountains, CHR 509911; *D. Glenny* 6843, Gertrude Valley, CHR 530520; *D. Glenny* 6876, Routeburn Valley, CHR 530552; *D. Glenny* 6838, Lake Marion, CHR 530513; *D. Glenny* 6884, Rees Valley, CHR 559445; *P. N. Johnson* 1377, Lake Manapouri, CHR 512377; *P. N. Johnson* 1407, Livingstone Mountains, CHR 515002.

CONSERVATION STATUS: Widespread and common.

ETYMOLOGY: Named for A. H. R. Grisebach, a German botanist who worked on *Gentiana* (Grisebach 1845).

ILLUSTRATIONS: Wilson (1978, p. 175); Wilson (1982, p. 248); Mark & Adams (1973, p. 173).

DISCUSSION: Included in *G. grisebachii* is the A. P. Druce tag name *Gentiana* "rimutaka", which Druce applied to small to intermediate-sized plants from all parts of *G. grisebachii*'s range in the North Island, while maintaining the name *G. matthewsii* for larger plants from the North Island. Plants to which Druce applied the tag name *G.* "rimutaka" are sometimes found in forest openings in the Rimutaka and Ruahine ranges on soils that are well drained and are prone to drying in summer, but these are not morphologically distinct from wetland plants belonging to the species.

Gentianella impressinervia Glenny, sp. nov.

DIAGNOSIS: *Gentianellae montanae* similis et affinis, sed habitu robustiore, caudice longo, ramoso, caulibus hornotinis adventitiis ex caudice orientibus, nervis foliorum medianis atque lateralibus supra impressis, antheris magnis, 2.8–3.9 mm longis, discrimine singulari inter congeneres novozelandicos coloris tubi corollini flavi differt.

HOLOTYPE: *K. Ford B/5*, Paparoa Range, Buckland Peaks, summit, 1326 m, 24 March 1996, CHR 526448 (Fig. 62).

DESCRIPTION: Plants polycarpic, height in flower(160–)350–600 mm. Caudex branched, 65–300 mm long, leaf scars conspicuous, stolons usually present. Root 2.9–4.5 mm diameter at stem base. Flowering stems terminal and lateral, 4–6 per plant, largest flowering stem 2.5–5.5 mm diameter at base, 2.3–3.1 mm diameter when dry, stem colour tinted crimson, brown or bronze, lateral flowering stems erect, flowering stem leaves 2–7 pairs per stem, lowest pedicels from halfway up flowering stem or near apex of flowering stem. Rosette of leaves not distinct or distinct from flowering stem leaves; leaves elliptic or obovate, 18–61 mm long, (7.9–)12.7–21 mm wide, green or tinted crimson below, or slightly bronze-tinted, glossy, flat or slightly V-shaped in section, recurved or not, with lateral veins impressed on adaxial leaf surface; leaf apex apiculate or rounded; petiole absent or indistinct, 3.5–5.5 mm wide at leaf base. Flowering stem

leaves ovate or obovate as for rosette leaves but sessile and almost amplexicaul, c. 19 × 12 mm. Pedicels 1 or 2 per leaf axil, (12–)19–35 mm long, 1.1–1.4 mm diameter, 0.45–0.55 mm diameter when dry. Flowers (6–)13–30(–42) per plant, (19–)21–24 mm long, rarely female. Calyx (7.9–)10.5–12.7 mm long, green, hairs at calyx-corolla fusion line present; lobes 6.6–9.4 mm long, (2.9–)3.5–3.7 mm wide at base, plane, apices acute, margins smooth, sinus hairs absent, sparse, or abundant. Corolla (16–)19–24 mm long; tube yellow or yellow-green, 4.6–7.2 mm long; lobes white with veins uncoloured, (11.3–)14.3–18.1 mm long, (7.5–)11.2–12.5 mm wide, hairs below sinus present; nectary 1.2–2.2 mm from corolla base, dark yellow. Filaments (9.0–)10.5–11.5 mm long from corolla base, (1.2–)1.5–1.7 mm wide. Anthers 2.8–3.9 mm long, anther wall bluish-purple, mouth yellow, extrorse at anthesis; pollen yellow. Stigma colourless. Ovules 44–60–84 per ovary, ovary yellow in maturity. Capsule 20–23 mm long. FL. Feb–Mar.

DISTRIBUTION (Fig. 63): NELSON: Glasgow Range, Lyell Range, Mt Mantell, Mt Zetland, Spenser Mountains, Brunner Range, Victoria Range. WESTLAND: Paparoa Range, Mt Mason. CANTERBURY: Upper Hope Valley, Mt Trovatore, Doubtful Range, Crawford Range.

HABITAT: Tall alpine tussocklands on ridges and hillslopes near ridges of *Chionochloa pallens*, less often in short grasslands of *C. australis* on ridges; with *Celmisia petiolata*, *C. armstrongii*, *C. dallii*, *Hebe odora*, *Dracophyllum rosmarinifolium*, *Astelia petriei*, *A. nivicola*, *Aciphylla hookeri*, *A. colensoi*, *Gentianella montana* var. *stolonifera*, *Ranunculus lyallii*, *Hebe venustula*, *Schoenus pauciflorus*, and *Blechnum montanum*; 1000–1500 m.

CHROMOSOME NUMBER: $2n = 36$ (as *Gentiana montana* var. *montana*, CHR 200894, in Hair et al. 1980).

RECOGNITION: By its height (350–600 mm), the much branched robust caudex with a rosette of leaves at the base of each flowering stem, the thick, broadly elliptic to obovate leaves with apiculate or rounded apices and glossy upper surface, with three impressed veins on the upper surface; the large flowers (c. 21–24 mm long), and the large anthers (2.8–3.9 mm long). Closest in appearance to *G. montana* subsp. *montana* and var. *stolonifera* (Table 20). It differs from *G. montana* in having a yellow corolla tube.

From *G. montana* s. s. it differs in usually having stolons (common on larger, older plants), older specimens are more branched and have a longer caudex with the leaf scars more conspicuous. *G. impressinervia* is larger in all aspects and has broader, more obovate leaves. It is often found with *G. montana* var. *stolonifera* and both have stolons but *G. impressinervia* has wider leaves, (7.9–)12.7–21 mm wide, not 3.5–10.5 mm wide, the plants are often taller (usually 350–600 mm, not 70–250–510 mm), and the flowers are larger in most dimensions (e.g., the corolla tube is 4.6–7.2 mm long, not 3.7–4.7 mm long, the nectary is 1.2–2.2 mm from the corolla base, not 0.5–1.3 mm, the anthers are 2.8–3.9 mm long, not 1.8–2.9 mm, and the filaments are (1.2–)1.5–1.7 mm wide, not 0.7–1.0 mm wide).

SPECIMENS EXAMINED: *D. Glenny* 6908, Trent Saddle, CHR 559466; *G. Jane*, Mt Fleming, CHR 526404; *M. Newfield*, Mt Technical, CHR 526413; *G. Jane*, Mt Mantell, CHR 516245.

CONSERVATION STATUS: Widespread and common in some localities, not threatened.

ETYMOLOGY: The name refers to the three clearly impressed veins seen on the upper surface of the leaves.

ILLUSTRATION: Salmon (1968, p. 233) labelled *Gentiana montana*.

DISCUSSION: This species has often been referred to as *G. montana*, or *G. montana* var. *stolonifera*. Referred to by Druce (1992a) as *Gentiana* "Paparoa".

Gentianella lilliputiana (C.Webb) Glenny, comb. nov.

Basionym: *Gentiana lilliputiana* C.Webb, *New Zealand J. Bot.* 28: 1 (1990). Lectotype (here chosen): *D. Bruce*, Central Otago, Dunstan Mountains, Upper Lauder Creek, CHR 460522! plant on right of sheet. Isotypes: AD, AK, AKU, CANB, MEL, NSW, WELT. \equiv *Chionogentias lilliputiana* (C.Webb) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

DESCRIPTION: Plants monocarpic, annual, height in flower (6–)10–20(–25) mm. Caudex unbranched. Taproot slender. Flowering stems terminal only or terminal and lateral, 1–4 per plant, stem colour yellow, lateral flowering stems erect or decumbent, c. 0.6 mm diameter when dry; flowering stem leaves 1–2 pairs per stem, lowest pedicels from near

apex of flowering stem. Rosette of leaves absent from flowering plants, leaves linear or narrowly elliptic, (1.5–)3.5–8.0(–13) mm long, (0.5–)1.0–2.0 mm wide, flat, not recurved, petiole indistinct, 2–7 mm long, 0.4–0.6 mm wide at leaf base. Flowering stem leaves narrower than leaves. Pedicels 0.7–1.7 mm long, c. 0.5 mm diameter, c. 0.45 mm diameter when dry. Flowers 1(–4) per plant, 3.7–5.0 mm long. Calyx 2.4–6.2 mm long, green tinted purple-black, hairs at calyx-corolla fusion line absent; lobes 1.0–3.3 mm long, 0.95–2.1 mm wide at base, plane, apices acute, margins smooth, sinus hairs absent. Corolla 3.4–4.3 mm long, white, veins uncoloured; tube 1.4–3.2 mm long; lobes 2.0–3.6 mm long, 1.3–2.3 mm wide, hairs below sinus absent; nectary 0.6–1.0 mm from corolla base. Filaments 1.9–4.1 mm long from corolla base, 0.2–0.3 mm wide. Anthers 0.4–0.7 mm long, introrse at anthesis. Ovules 2–4(–13) per ovary. Stigma colour unknown. Capsule 4.0–6.0 mm long. FL. Jan–Feb.

DISTRIBUTION (Fig. 47): CANTERBURY: Kirkliston Range, Hawkdun Range.

OTAGO: Dunstan Range.

HABITAT: Bogs and flushes in alpine grasslands and herbfields on rounded ridgetops; with *Abrotanella caespitosa*, *Isolepis aucklandica*, *Psychrophila obtusa*, *Coprosma atropurpurea*, *Oreobolus pectinatus*, and *Drepanocladus fluitans*; 1200–1800 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: By its very small size, with a single terminal flower; by its often having 4-merous flowers. It most closely resembles *G. filipes* of Nelson in size, but in Otago cushion bogs it is most likely to be confused with *G. amabilis*. It is annual, whereas *G. amabilis* is perennial, and the leaves are flat, not V-shaped in section. It is smaller in all dimensions than *G. amabilis* with leaves only 0.5–2.0 mm wide (2.5–12 mm wide in *G. amabilis*), the flowers are much smaller, 3.7–5.0 mm long (not 15–23 mm long), the corolla is only 3.4–4.3 mm long (not 12–23 mm long), and the anthers are very small, 0.4–0.7 mm long (not 1.7–3.0 mm long) and are introrse during the male phase.

SPECIMENS EXAMINED: *D. Bruce*, Dunstan Mountains, CHR 418480, 461347; *A. F. Mark*, Dunstan Mountains, OTA 041684; *A. Mark & R. Allen*, Dunstan Mountains, CHR 417292.

CONSERVATION STATUS: "Range restricted" in the classification of Molloy et al. (2001). Apparently quite abundant where it is found.

ETYMOLOGY: The epithet refers to the small size of this species.

ILLUSTRATION: Webb (1990, p. 2).

DISCUSSION: The pollen grains of *G. lilliputiana* are the most distinctive of any New Zealand species, being very finely reticulate. They resemble those of *G. magellanica*, and small plants of *G. magellanica* bear a strong resemblance to *G. lilliputiana*, but their DNA sequences indicate that these similarities are not due to a common ancestry. A suspected hybrid, *G. amabilis* × *G. lilliputiana* (D. Bruce, CHR 461350), has 9% of its pollen unstainable.

Gentianella lineata (Kirk) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 61 (1993).

Basionym: *Gentiana lineata* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 334 t. 27 (1895). Lectotype (here chosen): T. Kirk, Southland, Longwood Range, WELT 4708! plant at upper right of sheet. Isolectotypes: AK 7161 & 7163!

≡ *Chionogentias lineata* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

≡ *Oreophylax lineatus* (Kirk) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

= *Gentiana verecunda* Simpson, *Trans. & Proc. New Zealand Inst.* 79: 334 (1942).

Holotype: *G. Simpson*, Lake Manapouri, Mt Wilmott, 1200 m, in cushions of *Oreobolus* and *Donatia*, CHR 75699!

DESCRIPTION: Plants polycarpic, height in flower (30–)70–100(–180) mm. Caudex branched, stolons absent or present. Root much branched. Flowering stems terminal and lateral, 1–10(–18) per plant, largest flowering stem 0.9–1.0 mm diameter at base, c. 0.5 mm diameter when dry, stems tinted purple-black, lateral flowering stems erect or decumbent, flowering stem leaves 0–1 pairs per stem, lowest pedicels from near base of flowering stem to near apex of flowering stem. Rosette of leaves absent or present and distinct from flowering stem leaves, basal leaves narrowly elliptic or elliptic, leaf apex acute, 11–16 mm long, 1.2–3.0 mm wide, green or tinted crimson below or tinted purple-black, flat, not recurved; petiole indistinct to distinct, 4.5–10.4 mm long, 0.5–0.8 mm wide at leaf base. Flowering stem bracts absent, rarely with one pair. Pedicels

10–74 mm long (elongating after flowering to 30–120 mm), 0.5–0.8 mm diameter, 0.4–0.7 mm diameter when dry. Flowers 1–10(–18) per plant, 7.7–10.0 mm long. Calyx 6.4–9.0 mm long, green tinted purple-black, hairs at calyx-corolla fusion line few; lobes 4.9–7.0 mm long, 1.1–1.7 mm wide at base, plane, apices acute, margins smooth, sinus hairs absent. Corolla 4.6–10.5 mm long, white, veins uncoloured; tube 1.1–2.9 mm long; lobes 3.7–8.1 mm long, 2.0–4.6 mm wide, hairs below sinus absent; nectary 0.5–0.6 mm from corolla base. Filaments 2.4–6.0 mm long from corolla base, 0.35–0.45 mm wide. Anthers (0.8–)0.9–1.2(–1.5) mm long, anther wall blue-black, mouth yellow, introrse at anthesis; pollen yellow. Stigma colourless. Ovules 40–56 per ovary, ovary yellow in maturity. Capsule 7.3–14.2 mm long. FL. mid-Nov–Jan.

DISTRIBUTION (Fig. 64): OTAGO: Lammerlaw Range, Blue Mountains, Ajax Bog. SOUTHLAND: Fiordland (Dusky Sound, Mt Wilmott, Mt George, Oomah Valley, Lake Wapiti), Otautau, Longwood Range, Awarua Bog, Waituna Lagoon. STEWART ISLAND: Rakeahua, Table Hill, Granite Knob, Mt Anglem, Big South Cape Island, Pegasus Bay, Tin Range.

HABITAT: Coastal bogs, subalpine forest, alpine tussocklands, often on peat soils, with *Schoenus pauciflorus*, *Chionochloa pungens*, *Astelia linearis*, *Donatia novae-zelandiae*, and *Oreobolus pectinatus*; 0–1300 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980, Dawson & Beuzenberg 2000).

RECOGNITION: A small species with many branches; the flowering stems are usually without bracts and have solitary flowers. The leaves are smaller and narrower than most gentian species. Most similar in size to *G. filipes* and *G. lilliputiana* but neither of these species has a branched caudex. Small specimens and small-leaved specimens of *G. grisebachii* resemble *G. lineata*, especially in the calyx lobes, which in both species are long and narrowly acute, but *G. grisebachii* has leaf bracts below the flowers while this species usually has none.

VARIATION: Varies considerably in the length of flowering stems and the diameter of plants, probably due to soil fertility and plant age.

SPECIMENS EXAMINED: *D. Glenny* 6356, Mt Anglem, CHR 509879; *D. Glenny* 7475, Lake Wapiti, CHR 560102; *P. N. Johnson*, Ajax Bog, CHR 364169; *G. Simpson*, Mt

Wilmott, CHR 76316; *C. J. Webb* 78/17, Granite Knob, CHR 327342.

CONSERVATION STATUS: Widespread, not uncommon and not threatened.

ETYMOLOGY: *Lineata* describes the leaves, which are narrowly elliptic.

ILLUSTRATION: Kirk (1895 plate 27); Wilson (1982, p. 48).

Gentianella luteoalba Glenny sp. nov.

DIAGNOSIS: Ab *Gentianella divisa* foliis angustioribus, 4.2–5.2 mm latis (non 7.5–21 mm latis), ad medium folii non ampliatis, capsulis paucioribus, 5.6–7.5 mm longis (non 15–17 mm longis), ovulis paucioribus, 9–20 per ovarium, filamentis angustioribus, 0.6–0.8 mm latis, calice brevior, 6.7–8.4 mm longo distinguenda.

HOLOTYPE: *D. Glenny* 7361, Nelson, Lookout Range, 1400 m, 15 Feb 1998, CHR 559987 (Fig. 65).

DESCRIPTION: Plants monocarpic, biennial, height in flower 25–60 mm (rosette of leaves compact, 22–70 mm diameter). Caudex unbranched, to 55 mm long. Root 2.2–4.4 mm diameter at stem base. Flowering stems terminal, largest flowering stem 3.0–5.0 mm diameter at base, stem colour green or tinted purple-black, flowering stem leaves 1 pair per stem, lowest pedicels from near base of flowering stem to halfway up flowering stem. Rosette of leaves present but not very distinct or present and distinct from flowering stem leaves, leaves lingulate, 10.5–33 mm long, 4.2–5.2 mm wide, green, margins dark red-brown, channelled, recurved or not, leaf apex rounded; petiole absent, leaf 2.7–5.0 mm wide at base. Pedicels 1 per leaf axil, 1–21 mm long, 1.0–1.3 mm diameter. Flowers 14–133 per plant, 12.5–19.5 mm long. Calyx 6.7–8.4 mm long, green, tinted brown, hairs at calyx-corolla fusion line present; lobes 4.8–5.9 mm long, 2.2–2.9 mm wide at base, plane, apices acute, margins smooth or minutely serrulate at lobe base or for full length of margin, sinus hairs sparse to abundant. Corolla 11.6–14.9 mm long, uniformly pale yellow; tube 3.8–4.7 mm long; lobes 9.2–10.2 mm long, 5.1–6.3 mm wide, hairs below sinus present; nectary 1.5–2.0 mm from corolla base. Filaments 7.8–9.9 mm long from corolla base, 0.6–0.8 mm wide. Anthers 1.0–2.1 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis; pollen yellow. Stigma

colourless. Ovules 9–20 per ovary, ovary turning slightly blue in maturity. Capsule 5.6–7.5 mm long. FL. Feb–Mar.

DISTRIBUTION (Fig. 60): NELSON: Lookout Range, northern end of Hope Range.

HABITAT: Almost bare granite gravel exposures on rounded ridgetops, with *Chionohebe pulvinaris*, *Dracophyllum pronum*, *Luzula pumila*, and *Poa colensoi*; 1200–1600 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: There is no other species in the Nelson region with which this could be confused. Its nearest relative in Nelson is *G. filipes*, which has smaller, narrower leaves and smaller flowers. *G. divisa* is also very similar (Table 19) but is not present in Nelson.

VARIATION: A very uniform species, consistent with its small range.

SPECIMENS EXAMINED: *G. Jane*, Hope Range, CHR 516247, *C. J. Webb 76137*, Lookout Range, CHR 283742.

CONSERVATION STATUS: "Nationally vulnerable" in the classification of Molloy et al. (2001), as the total population size would be under 5000 in an area under 100 ha. The number of plants were estimated in the field to be in the thousands, occupying all available habitat. There appear to be no threats to this large population.

ETYMOLOGY: Refers to the uniformly pale yellow corolla, a feature not possessed by any other Australasian species of *Gentianella*.

DISCUSSION: An outcrossing species despite its small ovule number. Bumblebees were observed visiting the flowers on the remote Lookout Range.

Gentianella magnifica (Kirk) Glenny comb. et stat. nov.

Basionym: *Gentiana bellidifolia* var. *magnifica* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 337 (1895). Lectotype (here chosen): *T. K[irk]*, near the summit of Mount Captain, Amuri, 4,500 feet, WELT 4715! plant on right side of sheet.

≡ *Gentiana divisa* var. *magnifica* (Kirk) Allan, *Flora New Zealand* 1, 772 (1961).

DESCRIPTION: Plants monocarpic or polycarpic, biennial or perennial, height in flower 75–190 mm. Caudex unbranched, 70–80 mm long. Root 8–13 mm diameter at stem base and 400–800 mm long. Flowering stems terminal and lateral, 10–40 per plant, terminal flowering stem 5.7–7.3 mm diameter at base, green; lateral flowering stems erect; flowering stem leaves 2–6 pairs per stem, lowest pedicels from near apex of flowering stems. Rosette of leaves absent from flowering plants, lower stem leaves narrowly elliptic, 35–105 mm long, 10.0–15.5 mm wide, green, margins sometimes crimson, flat or channelled, apex acute; petiole absent, leaves 4.4–9.2 mm wide at base. Flowering stem leaves narrowly ovate. Pedicels 1 per leaf axil, 10–52 mm long, 1.4–1.5 mm diameter. Flowers 45–220(–256) per plant, 19–26 mm long. Calyx 12.3–20 mm long, green, hairs at calyx-corolla fusion line absent or present; lobes 8.5–10.0(–14.5) mm long, 4.3–5.4 mm wide at base, plane, apices acute, margins smooth, sinus hairs abundant. Corolla 17.2–24.5 mm long, white, veins uncoloured; tube 4.7–8.1 mm long; lobes 12.4–16.4 mm long, 8.0–10.8 mm wide, hairs below sinus present; nectary 1.6–3.3 mm from corolla base. Filaments 10.7–16 mm long from corolla base, 1.2–1.5 mm wide. Anthers 2.0–2.9 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis; pollen yellow. Stigma colourless. Ovules 9–23(–37) per ovary, ovary turning dark purple in maturity. Capsule 19–25 mm long. Seeds 1.1–1.5 mm diameter. FL. Mar.

DISTRIBUTION (Fig 60): MARLBOROUGH: Rachel Range (Barefell). CANTERBURY: Hanmer Range (Mt Captain, Miromiro).

HABITAT: Alpine scree, invariably of finely shattered black argillite; with *Rachelia glabra* and *Haastia sinclairii*; 1420–1700 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: Most similar to *G. divisa* but larger in most dimensions (Table 18). However, the ovules are fewer, 9–23 per ovary, (29–56 per ovary in *G. divisa*), while the seeds are larger, 1.1–1.5 mm diameter (c. 0.74 mm diameter in *G. divisa*).

VARIATION: The few specimens available are similar to each other except for one

specimen from Barefell that is very large in all floral and seed dimensions.

SPECIMENS EXAMINED: *D. Glenny* 6900, 7451, Mt Barefell, CHR 530573, 529216; *J. McLintock*, Barefell, CHR 526300; *D. Petrie*, 8/11/1914, Miromiro, 5200 ft, CANU 2931.

CONSERVATION STATUS: "Nationally endangered" in the classification of Molloy et al. (2001) as it is only known recently from a single site with under 1000 individuals. There appear to be no threats to this population.

ETYMOLOGY: "Magnificent", probably so named for its size and many flowers.

ILLUSTRATION: Fig. 66.

DISCUSSION: This species is most closely related to *G. divisa* but is larger, and more similar to *G. corymbifera* subsp. *corymbifera* in some of its dimensions. I was unable to find plants on Mt Captain, although large areas of black argillite scree are present there. It was last collected on the Hanmer Range by Petrie in 1914. It was referred to as *Gentiana* "Barefell" by Druce (1992b). There is a brief flowering in the first half of March. This species seems to flower about every 3 years. At Barefell the flowers are heavily preyed upon by an insect, something rarely seen in New Zealand *Gentianella* and this predation may account for its masting behaviour.

Gentianella montana (G.Forst.) Holub, *Folia Geobot. Phytotax.* 2: 117 (1968).

Basionym: *Gentiana montana* G.Forst., *Prodromus* p. 21 (1786). Lectotype (chosen by Adams 1995, p. 977): *G. Forster*, Dusky Sound, BM, annotated "Type" by N. E. Brown. Isolectotype: P.

≡ *Oreophylax montanus* (G.Forst.) Á.Löve, *Taxon* 32: 511 (1983) nom. inval.

≡ *Chionogentias montana* (G.Forst.) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

DESCRIPTION: Plants polycarpic or monocarpic and biennial, height in flower (45–)70–570 mm. Caudex unbranched or branched, 10–160 mm long, with leaf scars. Stolons present or absent. Flowering stems single and terminal or multiple and both terminal and lateral, 1–23 per plant; largest flowering stem 1.4–6.1 mm diameter at base, 1.4–4.1 mm diameter when dry, green, tinted crimson, purple-black, or bronze,

flowering stems erect from a decumbent base, flowering stem leaves 2–7, lowest pedicels from near the base to near the apex of stem. Rosette of leaves usually distinct, leaves narrow rhomboid, elliptic, or orbicular, 14–98 mm long, 3.5–18 mm wide, flat or V-shaped in section, not recurved, bronze or crimson below; apex acute or rounded; petiole indistinct or distinct and 9–45 mm long, 1.4–7.5 mm wide at narrowest point. Pedicels 1–2 per leaf axil, 5–38 mm long, 0.8–2.0 mm diameter, 0.5–1.1 mm diameter when dry. Flowers 1–49(–120) per plant, 17–20 mm long. Calyx 6.6–11.8 mm long, green or tinted crimson or purple-black, hairs at calyx–corolla fusion line present; lobes 4.4–9.6 mm long, 1.8–4.0 mm wide at base, plane, apices acute, margins convex, smooth or minutely serrulate, sinus hairs absent or present. Corolla 11–24 mm long, white, veins purple or uncoloured; tube 2.3–5.0 mm long; lobes 10–16 mm long, 5.4–11.3 mm wide, hairs below sinus absent or present; nectary 0.4–1.3 mm from corolla base. Filaments 6–11 mm long from corolla base, 0.6–1.8 mm wide. Anthers 1.7–3.2 mm long, anther wall blue-black, mouth yellow, extrorse, rarely horizontal at anthesis; pollen yellow. Stigma colourless, or blue to violet. Ovules 32–88 per ovary. Capsule 15–28 mm long.

KEY TO SUBSPECIES

- 1 stigma blue or violet; corolla always white with purple veins; plants invariably biennial; North Island from Tararua Range to Hikurangi subsp. *ionostigma*
 stigma colourless; corolla usually white with colourless veins; plants usually perennial, sometimes biennial; South Island subsp. *montana*

subspecies *ionostigma* Glenny, subsp. nov.

DIAGNOSIS: Ab subspecie *montana* statu solummodo bienni, habitu minore, 45–310 mm alto, capsulis minoribus 17.0–20.3 mm longis, venis corollae purpureis, stigmatibus caesio vel violaceo differt.

HOLOTYPE: *D. Glenny* 6795, Wellington L. D., Whana Huia Range, CHR 559363.

DESCRIPTION: Plants monocarpic and biennial, height in flower (45–)80–157–270(–310) mm. Caudex unbranched, 15–100 mm long, stolons absent or rarely present. Root 0.8–2.2 mm diameter at stem base. Flowering stems usually terminal only, sometimes

terminal and lateral, 2–6 stems per plant, largest flowering stem 1.9–3.1 mm diameter at base, 1.4–2.8(–4.3) mm diameter when dry, stems tinted crimson or tinted purple-black, lateral flowering stems erect or decumbent, flowering stem leaves 2–5 pairs per stem, lowest pedicels from near base of flowering stem to near apex of flowering stem. Rosette of leaves distinct from flowering stem leaves to indistinct, leaves elliptic or ovate, 13–38(–55) mm long, 4.1–12(–17) mm wide, tinted crimson or purple-black below, apex acute to rounded, leaf flat with a V-shaped petiole, V-shaped in section or channelled; petiole indistinct to distinct, 6.4–15.3 mm long, 1.2–3.0 mm wide at narrowest point. Pedicels 1 per leaf axil, rarely two, 8–35 mm long, 0.8–1.4 mm diameter, 0.5–0.8 mm diameter when dry. Flowers 4–35(–55) per plant, 11.5–20 mm long. Calyx 6.6–11.9 mm long, green tinted purple-black at the lobe apices; lobes 4.6–9.2 mm long, 1.9–3.0 mm wide at base, plane, apices acute, margins smooth, sinus hairs sparse or absent. Corolla 11.0–19.3 mm long, white, veins purple or violet; tube 2.3–4.6 mm long; lobes 8.5–15.3 mm long, 5.4–8.5 mm wide, hairs below sinus present; nectary 0.4–1.2 mm from corolla base. Filaments 7.4–9.8 mm long from corolla base, 0.7–1.0 mm wide. Anthers 1.8–2.9 mm long. Stigma blue, blue-grey or violet. Ovules 44–88 per ovary. Capsule 17–22(–25) mm long. FL. Jan–Feb.

DISTRIBUTION (Fig. 67): GISBORNE: Raukumara Range (Hikurangi, Arowhenua, Honokawa, Maungawaru Plateau), Huiarau Range, Maungapohatu. HAWKES BAY: Kaweka Mountains. WELLINGTON: Erua, Kaimanawa Mountains, Ruahine Range, Tararua Range.

HABITAT: Alpine and subalpine, mostly on peat soils in valley head basins, *Schoenus pauciflorus*, *Carpha alpina*, *Oreobolus pectinatus*, *Phyllachne colensoi*, and *Sphagnum falciculatum* mossfield and cushionfield, with *Drepanocladus aduncus*, *Coprosma perpusilla*, *Gentianella bellidifolia*, and *Euphrasia cuneata*; also in subalpine shrublands of *Olearia colensoi*, *Griselinia littoralis*, *Phormium cookianum*, *Brachyglottis elegnifolius*, and *Ozothamnus leptophyllus*; 1050–1470 m.

CHROMOSOME NUMBER: $n = 18$ (Post 1983 based on two counts).

RECOGNITION: This subspecies belongs to *G. montana* by virtue of its terminal flowering stems, the presence of stolons on some plants, the crimson tinting of the stem and abaxial leaf surface, and the convex curve of the calyx lobe margins. From other

subspecies of *G. montana* it can be distinguished by the blue to violet stigmas, by the purple corolla veins, the smaller plants (45–310 mm tall, not (120–)170–570 mm tall in subsp. *montana* and 70–510 mm in var. *stolonifera*) and smaller capsules that are 17–20 mm long (20–26 mm long in subsp. *montana* and 15–28 mm long in var. *stolonifera*). In the North Island, this subspecies is most similar to *G. bellidifolia*, and shares the same habitat, and also has purple corolla veins there. *G. montana* subsp. *ionostigma* can be distinguished from *G. bellidifolia* by the terminal flowering stem, the blue to violet stigma, and the crimson to purple-black tinting of the underside of the leaf. It is also similar to *G. chathamica* subsp. *nemorosa*, which also has a blue stigma and purple corolla veins. It differs from *G. chathamica* subsp. *nemorosa* in the field by its preference for open habitat and its more erect lateral flowering stems. On close examination, it differs in having a longer corolla (11–19 mm, not 7–10 mm) and longer capsules (17–25 mm, not 7–10 mm), and has calyx sinus hairs (absent in *G. chathamica* ssp. *nemorosa*). It is also similar to *G. grisebachii*, from which it differs in having shorter pedicels and a distinct rosette of leaves.

VARIATION: Plants vary in size considerably, the smallest plants occurring in very wet bogs. No geographic variation is evident.

SPECIMENS EXAMINED: *M. J. Bayly* 571, 572, 573, Mt Holdsworth, CHR 526394; *I. Breitwieser* 2062, Mt Hikurangi, CHR 526397; *D. Glenn* 6794, 6798, 6799, Whana Huia Range, CHR 559362, 559365, 559366.

CONSERVATION STATUS: Common in the alpine zone, at least in the southern North Island ranges.

ETYMOLOGY: *Ionostigma* means violet stigma.

ILLUSTRATIONS: Salmon (1968, p. 234, plates 319 and 320); Salmon (1991, p. 240, plate 1000) shows flowers of this subspecies.

subspecies *montana*

= *Gentiana spedenii* Petrie, *Trans. & Proc. New Zealand Inst.* 56: 14 (1926). Holotype: *J. Speden*, Princess Range, 4000 ft, 26/1/24, "purple or violet flower", WELT 4720!

= *Gentiana tereticaulis* Petrie, *Trans. & Proc. New Zealand Inst.* 49: 51 (1917).

Lectotype (here chosen): *D. P[etrie]*, Lake Harris, Routeburn, nr. Lake Wakatipu, 27:2:11, WELT 2723a! plant on right of sheet. Isolectotypes: WELT 2723b, AK 7191! The AK specimen is ex herb. Cheeseman and is undated.

≡ *Gentianella tereticaulis* (Petrie) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 65 (1993).

≡ *Chionogentias tereticaulis* (Petrie) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

= *Gentiana bellidifolia* var. *pulchella* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 336 (1895). Lectotype (here chosen): *T. Kirk*, Arthur's Pass, WELT 4717!

DESCRIPTION: Plants polycarpic or monocarpic and biennial, height in flower 70–570 mm. Caudex 10–160 mm long. Stolons present or absent. Root 1.2–9 mm diameter at stem base. Flowering stems 1–23 per plant, largest stem 1.4–6.1 mm diameter at base, 0.5–4.1 mm diameter when dry, stem colour green, crimson, or purple-black, lateral flowering stems erect or decumbent, flowering stem leaves 2–7 pairs per stem. Rosette(s) of leaves usually distinct. Rosette leaves 14–98 mm long, 3.5–18 mm wide, green or tinted crimson below; petiole 15–45 mm long, 1.6–7.5 mm wide at leaf base. Pedicels 5–38 mm long (elongating to 55 mm), 0.9–2.0 mm diameter, 0.5–1.1 mm diameter when dry. Flowers 1–49 per plant, 11–20 mm long, rarely male-sterile. Calyx 7.5–11.8 mm long; lobes 5.3–9.6 mm long, 2.1–3.0 mm wide at base, sinus hairs absent, sparse or abundant. Corolla 13.5–20 mm long, white, veins usually uncoloured, rare purple; tube 2.6–5.0 mm long; lobes 10.0–16 mm long, 6.8–10.3 mm wide, hairs below sinus absent or present; nectary 0.4–1.4 mm from corolla base. Filaments 6.0–11.0 mm long from corolla base, 0.7–1.2 mm wide. Anthers 1.8–3.0 mm long, anther wall blue-black, mouth yellow. Stigma colourless. Ovules 40–84 per ovary. Capsule 15–28 mm long.

KEY TO VARIETIES

- 1 stolons rarely present; calyx hairs present; corolla tube white; plants perennial or biennial, particularly in the south of the South Island; distribution east of the alpine fault from Fiordland to North Westland and throughout Nelson, not usually on granite except in Fiordland var. *montana*
 stolons always present in a population; calyx hairs sometimes absent; corolla tube white or green; plants invariably perennial; distribution west of the alpine fault from Mt Hohonu to Mt Glasgow, usually on granite or quartzite
 var. *stolonifera*

var. *montana*

DESCRIPTION: Plants monocarpic and biennial, or polycarpic (rarely in Southland, usually in Nelson), height in flower (120–)170–570 mm. Caudex 10–90 mm long. Stolons sometimes present. Root 1.2–9 mm diameter at stem base. Flowering stems 1–23 per plant, largest stem 1.7–6.1 mm diameter at base, 1.6–4.1 mm diameter when dry, stem colour green or tinted crimson, lateral flowering stems erect or decumbent, flowering stem leaves 2–5 pairs per stem. Rosette of leaves (23–)37–98 mm long, (6.7–)9.4–18 mm wide, green or tinted crimson below; petiole 15–45 mm long, 1.6–7.5 mm wide at leaf base. Pedicels 11–38 mm long (elongating to 55 mm), 0.9–2.0 mm diameter, 0.5–1.1 mm diameter when dry. Flowers (2–)21–49 per plant, 11–19 mm long, rarely female. Calyx 7.5–11.2 mm long; lobes 5.3–9.6 mm long, 2.1–2.8 mm wide at base, sinus hairs sparse to abundant. Corolla 14.3–17.5 mm long, white, veins uncoloured, rarely purple; tube 2.6–5.0 mm long; lobes 11–16 mm long, 7.0–10.3 mm wide, hairs below sinus absent or present; nectary 0.4–1.4 mm from corolla base. Filaments 6.9–11.0 mm long from corolla base, 0.7–1.2 mm wide. Anthers 2.0–3.0 mm long, wall blue-black, mouth yellow. Ovules 40–84 per ovary. Capsule 20–26 mm long. FL. mid-Jan–Mar.

DISTRIBUTION (Fig. 68): NELSON: Goulard Downs, McKay Downs, Perry Saddle, Lead Hills, Cobb Valley and surrounding ranges, Red Hills, Mt Arthur Range, Mt Owen, Hope Range, Lookout Range. MARLBOROUGH: Raglan Range, Richmond Range, Mt Riley. CANTERBURY: Island Pass, Lake Tennyson, Spenser Mountains, Lake Sumner, Torlesse Range, Arthur's Pass, Avoca Valley. WESTLAND: Mt Alexander, Kelly Range, Browning Pass, Lord River, Burster Range, Mt Fox, Cook River, Burton Range, Alex Knob, Copland Valley, Lake Sweeney, Gorge River, Cascade River, Olivine Range. OTAGO: Okuru River, Red Hills, Skippers Range, Wilkin Valley, Headlong Spur, Humboldt Mountains. SOUTHLAND: Longwood Range, throughout Fiordland: Doubtful, Dusky, Caswell, and Milford sounds, Hump Ridge, Princess Range, Mt Burns, Manapouri, Tutuko Valley. Most common in Fiordland and Nelson but scattered along the central Southern Alps.

HABITAT: Alpine tussocklands of *Chionochloa pallens*, *C. rubra*, *C. teretifolia*, and *C. crassiuscula*, on hillslopes and in depressions; scrub and shrublands of *Dracophyllum longifolium*, *Phyllocladus alpinus*, *Halocarpus biformis*, *Archeria traversii*,

Brachyglottis rotundifolia, *Pseudopanax colensoi*, *Hebe mooreae*, and *Coprosma crenulata*, with *Pentachondra pumila*, *Oreobolus pectinatus*, *Astelia nivicola*, and *Sphagnum cristatum*; in well drained, moist or wet and peaty soils; 740–1535 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980, Dawson & Beuzenberg 2000); $n = 18$ (Post 1983).

RECOGNITION: *G. montana* ssp. *montana* can be recognised by a combination of characters: the crimson colour of the undersurface of the leaf, the white corolla, the terminal flowering stems, the tall upright flowering stems that are often crimson, by the convex margins of the calyx lobes, and by the alpine tall tussockland habitat. In Nelson, this subspecies is similar to *G. corymbifera* and both share the same tall tussockland habitat and are particularly difficult to tell apart there. The petiole of *G. montana* is narrower (1.6–7.5 mm) than in *G. corymbifera* subsp. *corymbifera* (4–18 mm wide). The calyx lobes are narrower at the base (2.1–2.6 mm) than in *G. corymbifera* subsp. *corymbifera* (3.2–3.4 mm) and characteristically have margins that are convex, somewhat resembling a gothic arch (Fig. 4) in common with all other members of the *G. montana* group of species, while in *G. corymbifera* they are triangular with straight to concave margins (Fig. 5). *G. montana* also has some similarities with *G. spenceri*: the crimson tinting of leaves and stems and the presence of both terminal and lateral flowering stems. *G. spenceri* differs from *G. montana* in having purple corolla veins, short pedicels, it is a smaller plant, and is monocarpic. In South Westland, *G. montana* is difficult to distinguish from large forms of *G. grisebachii*, but *G. montana* develops multiple rosettes while *G. grisebachii* never does. In general, small specimens of subsp. *montana* with a very short caudex are likely to give the most difficulty.

VARIATION: *G. montana* subsp. *montana* shows considerable variation over its geographical range, as indicated above. Monocarpy is common in Southland but not in Nelson. Most Western Otago and Southland plants appear to be monocarpic, but some are polycarpic (e.g., C. J. Webb 77030, Red Hills, CHR 322732). Nelson plants are more branched with an average of 3.0 stems per plant ($n = 50$); whereas Southland plants have an average of 1.8 stems per plant ($n = 50$). Plants in wet peat soils sometimes develop stolons (new shoots developing from old parts of the caudex) and have leaves with longer, narrower petioles. Plants of this type are common in red tussockland in the Heaphy area, are occasionally found elsewhere in Nelson, and Central

and South Westland, but are absent from Fiordland.

SPECIMENS EXAMINED: *D. Given* 72389, Wet Jacket Arm, CHR 230614; *D. Glenny* 6870 & 6873, Lake Harris, CHR 559431, 559434; *D. Glenny* 6818, Mt Mytton, CHR 559379; *D. Glenny* 6836, Mt Arthur, CHR 559397; *D. Glenny* 6882, Kea Basin, CHR 559443; *D. Glenny* 6840, West Homer Tunnel, CHR 559402; *D. Glenny* 6842, East Homer Tunnel, CHR 559406; *D. Glenny* 7349, Balloon Hut, CHR 560067; *D. Glenny* 7466, Lake Wapiti, CHR 560091; *P.N. Johnson* 1358, Borland, CHR 511786; *G. Spearpoint*, Haast, Headlong Spur, CHR 518957.

CONSERVATION STATUS: Widespread and common throughout its range, not threatened.

ETYMOLOGY: *Montana* means "of the mountains".

ILLUSTRATION: Fig. 69, showing a Nelson plant; Cave & Paddison (1999, p. 138) also shows a plant typical of its appearance in Nelson; Mark & Adams (1973, plate 75 — all three illustrations on the page).

DISCUSSION: Lectotypified by Adams (1995), the lectotype is a single lateral branch from a plant (shown in his plate on p. 990), making it difficult to be sure of its identity, but the calyx lobes have the appearance of *G. montana*. *G. tereticaulis* Petrie is certainly *G. montana*, as the population at the type locality (Lake Harris on the Routeburn Track) are in accord with other Southland populations. The type of *G. spedenii* is a depauperate specimen of *G. montana*. The only unusual feature of this specimen is that the label says "purple or violet flower", whereas I have never seen colour in the corolla of lower South Island populations of *G. montana*. Kirk's *bellidifolia* var. *pulchella* has two syntypes, one a collection from Arthur's Pass that is *G. montana*, and the other a collection from Meins Knob in the Rakaia Valley that is *G. bellidifolia*. Kirk gives the distribution as "Arthur's Pass, and other localities in the Canterbury Alps; 2,500 ft.–3,000 ft.". I have chosen the Arthur's Pass specimen as a lectotype, as the Meins Knob specimen is from 5 000 ft and so disagrees with the protologue despite its having "var. *pulchella*" in Kirk's handwriting.

var. *stolonifera* Cheeseman, *Man. New Zealand fl.* 451 (1906). Lectotype (here chosen): *W. Townson*, "Mount Rochfort, near Westport, 3000 ft, in scrub. Flowers white with

purple streaks", AK 200251! upper left plant on sheet.

= *Gentiana townsonii* Cheeseman, *Man. New Zealand fl.* 450 (1906). Lectotype (here chosen): W. Townson, Mount Rochfort, near Westport, alt. 3000 ft, AK 7213! plant at lower centre of sheet. Sheet annotated by L. M. Cranwell thus: "Type selected: Dec 1941 L. M. Cranwell" with the note: "agreed HHA 1/5/55").

≡ *Gentianella townsonii* (Cheeseman) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 65 (1993).

≡ *Chionogentias townsonii* (Cheeseman) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

DESCRIPTION: Plants polycarpic, height in flower 70–510 mm. Root 1.5–2.5 mm diameter at stem base. Caudex branched, 16–160 mm long. Stolons always present on older plants. Flowering stems 1–5 per plant; largest stem 1.4–3.2 mm diameter at base, (0.5–)1.2–1.9(–3.0) mm diameter when dry, green, crimson, or purple-black, flowering stem leaves 3–7 pairs per stem with sometimes a gradual transition from rosette leaves; lowest pedicels from near apex of flowering stem. Rosette leaves 14–42 mm long, 3.5–10.5 mm wide, usually tinted crimson below, otherwise bronze; apices rounded to acute; petiole when distinct 9.5–19 mm long, 1.4–3.2 mm wide at narrowest point. Pedicels 5–32 mm long, 1.0–1.5 mm diameter. Flowers 1–15 per plant, 17–20 mm long. Calyx 9.0–11.8 mm long; lobes 6.9–9.2 mm long, 1.8–3.0 mm wide at base, sinus hairs absent or sparse. Corolla 13.5–20 mm long, rarely purple; tube 2.9–4.7 mm long, usually green; lobes 10.0–15.3 mm long, 6.8–10.1 mm wide, white, veins uncoloured or purple, hairs below sinus present; nectary 0.5–1.3 mm from corolla base. Filaments 6.0–10.0 mm long from corolla base, 0.7–1.0 mm wide. Anthers 1.8–2.9 mm long, anther wall blue-black. Ovules 44–56 per ovary. Capsule 15–28 mm long. FL. (Jan–)Feb–Apr.

DISTRIBUTION (Fig. 68): NELSON: "Turks Cap Range", Glasgow Range, Denniston & Stockton plateaux, ridge north of Te Kuha, German Terrace, Mt Mantell, Paparoa Range from Buckland Peaks to Mt Sewell. WESTLAND: Hohonu Range, Mount Te Kinga.

HABITAT: Alpine short tussocklands of *Chionochloa australis*, with *Aciphylla hookeri*, *Cyathodes dealbata*, *Celmisia petiolata*, *C. discolor*, *Dracophyllum rosmarinifolium*, *Astelia petriei*; in cushion bogs of *Donatia novae-zelandiae*, *Phyllachne colensoi*; sometimes in *Chionochloa pallens* tussocklands, with *Hebe odora*, *Gentianella impressinervia*; rarely on pakihi of *Leptospermum scoparium*, *Empodisma minus*,

Gleichenia microcarpa, *Baumea rigida*; margins of scrub of *Metrosideros umbellata*, *Nothofagus solandri* var. *cliffortioides* and *Leptospermum scoparium*; 120–1320 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: This variety is difficult to distinguish from some variants of *G. montana* s. s. from wet habitats that are stoloniferous and much branched. A very variable variety in the leaf size and shape, and the degree of branching of the caudex. Small-leaved forms are closest to *G. vernicosa*, which is also sometimes stoloniferous. *G. montana* var. *stolonifera* differs in having larger leaves (14–42 mm × 3.5–10.5 mm, not (12.0–)14.5–30.5 × (1.9–)2.4–5.0(–6.0) mm). Var. *stolonifera* can resemble *G. impressinervia* in being much branched with a long caudex, but differs in having smaller leaves (18–61 mm × (7.9–)12.7–21 mm in *G. impressinervia*) and never has the yellow corolla tube that is a universal feature of *G. impressinervia*.

VARIATION: A variable taxon in which it is possible to recognise the geographical variants from their leaf shape alone. Plants from Buckland Peaks have the largest leaves. Plants from the montane pakihi have a long petiole with a diamond-shaped lamina and are sparsely branching, and in this respect are close to the common Fiordland form of *G. montana* s. s., but differ in being stoloniferous, which Fiordland *G. montana* never is.

SPECIMENS EXAMINED: *D. Glenny* 6458, 6448, Buckland Peaks, CHR 509983, 509975; *D. Glenny* 6418, Sewell Peak, CHR 509944; *D. Glenny* 6945, Mt Rochfort, CHR 526295; *G. Jane*, Mt Fleming, CHR 526404; *G. Jane*, Mt Mantell, CHR 516244; *P. Lockhart*, Buckland Peaks, CHR 526411.

CONSERVATION STATUS: Not threatened.

ETYMOLOGY: Refers to the stolons that are present in mature plants of this variety.

ILLUSTRATION: Cheeseman (1914, vol. 2, plate 139) as *G. townsonii*. The two illustrations of *G. townsonii* in Cheeseman's plate are not an exact match of any of Townson's collections at AK, but they could be a modification of those on Townson's specimen AK 7213.

Gentianella patula (Kirk) Holub, *Folia Geobot. Phytotax.* 3: 218 (1968).

Basionym: *Gentiana bellidifolia* var. *patula* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 330–341 (1895). Lectotype (here chosen): *T. Kirk*, Rotoiti, Nelson, Jan 1875, annotated *Gentiana bellidifolia* var. *patula* in Kirk's handwriting with red ink, WELT 47583! plant on right of sheet.

≡ *Gentiana patula* (Kirk) Cheeseman, *Man. New Zealand fl.* 452 (1906).

≡ *Chionogentias patula* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

DESCRIPTION: Plants monocarpic and biennial, or polycarpic, height in flower (60–)110–210–290(–370) mm. Root 2.7–6.3 mm diameter at stem base. Caudex unbranched or branched, 25–70 mm long; stolons absent. Flowering stems terminal and lateral, 1–36 per plant, largest flowering stem 1.1–2.4(–3.6) mm diameter at base, 1.6–3.6 mm diameter when dry, tinted crimson to purple-black, lateral flowering stems decumbent or erect, flowering stem leaves 3–4(–5) pairs per stem, lowest pedicels from near apex of flowering stem. Rosette of leaves distinct from flowering stem leaves, leaves elliptic, (18–)26–32–44 mm long, 3.5–6.5–9.0 mm wide, green, flat or V-shaped in section, recurved or not; leaf apex acute; petiole distinct, 10–29 mm long, 1.5–1.9–2.5 mm wide at leaf base. Flowering stem leaves ovate, apex acute, base clasping, strongly folded. Pedicels 1 or 2 per leaf axil, 9–35 mm long, 0.8–1.0 mm diameter, 0.5–0.6 mm diameter when dry. Flowers (3–)40–76–86(–126) per plant, 10–15 mm long. Calyx 5.1–6.7–8.5 mm long, green or green tinted purple-black, hairs at calyx-corolla fusion line present; lobes 3.4–4.3–6.0 mm long, 1.8–2.1–2.3(–2.6) mm wide at base, plane, apices acute, margins smooth, sinus hairs sparse. Corolla 5.9–12.7–15(–16) mm long, white or tinted pink or purple, veins uncoloured or purple; tube 3.0–3.5 mm long; lobes 9.0–11.4 mm long, 5.5–8.0 mm wide, hairs below sinus present; nectary 0.3–0.8 mm from corolla base. Filaments 4.5–7.5–8.8 mm long from corolla base, 0.7–0.9–1.0 mm wide. Anthers 1.7–2.1–2.4 mm long, anther wall blue-black, mouth yellow or orange-red, extrorse at anthesis or horizontal at anthesis. Stigma colourless or grey-violet. Ovules 24–33–44 per ovary. Capsule 12–15 mm long. FL. (Dec–)Jan–Mar(–May).

DISTRIBUTION (Fig. 17): NELSON: Cobb Valley, Takaka Hill, Moa Park, Gordons Knob, Beebys Knob, Travers Range, St Arnaud Range, Mt Mantell, Fairie Queen. MARLBOROUGH: Upper Wairau Valley (Hare Creek), Raglan Range, Island Pass. CANTERBURY: Clarence River valley near Lake Tennyson.

HABITAT: Valley floor tussocklands, grasslands and herbfields on roches moutonnées or alluvial fans, extending into scrub margins, associated with *Bulbinella hookeri*, *Chionochloa rubra*, *Agrostis tenuis*, *Dactylis glomerata*, *Poa colensoi*, *Uncinia rubra*. Also in *Chionochloa australis* and *C. pallens* alpine tussocklands on the mountains from Gordons Knob to Lewis Pass and Island Pass; 840–1524 m.

CHROMOSOME NUMBER: $n = 18$ (Post 1983, as *G. tereticaulis*), $2n = 36$ (Hair et al. 1980 as *Gentiana* sp., Cobb River, NW Nelson, CHR 102435).

RECOGNITION: Most similar to *G. montana*, *G. tenuifolia* and *G. spenceri* and growing with *G. tenuifolia* in the Cobb Valley. Most closely related to *G. montana* and sharing with that species a much branched caudex. Shorter than *G. montana*, with more flowering stems, and smaller flowers. Most *G. montana* populations have white flowers without coloured veins, while *G. patula* has white flowers in high altitude populations but flowers with coloured corolla veins at low altitude (820–1000 m). *G. patula* sometimes shares with *G. tenuifolia* purple corolla veins, and is found sometimes in similar valley floor habitats, but is not as tall and has smaller leaves. *G. patula* also sometimes shares with *G. spenceri* coloured corolla veins, but is taller than *G. spenceri* and has longer pedicels (8–15 mm on the terminal flower cluster, 20–35 mm on the flowers from lower bract axils). *G. tenuifolia* and *G. spenceri* often have coloured stigmas while *G. patula* rarely has a coloured stigma (see Malcolm & Malcolm 1988 p. 107 for comparison). *G. spenceri* and *G. tenuifolia* have an unbranched caudex while *G. patula* has the branched caudex of *G. montana* and its relatives, a feature particularly well developed in this species.

VARIATION: Clarence Valley and most Cobb Valley specimens share purple corolla veins, whereas other populations (Lake Sylvester, Canaan, Moa Park, Nelson Lakes, Upper Wairau, Lewis Pass) have uncoloured corolla veins. Clarence Valley specimens sometimes have a pink flush in the corolla. Clarence Valley specimens have crimson flowering stems while Cobb Valley specimens have purple-black flowering stems. The stigma is usually colourless, but the occasional plant has grey-violet stigmas. The number of flowering stems per plant varies considerably (from a single stem to 35 stems per plant, but averaging 10). Most plants appear to be monocarpic and biennial but the occasional plant in the Cobb Valley is polycarpic. At Cobb Valley and Lake Tennyson, this species flowers earlier than any other gentian, at the start of January, but may have a

second flowering in March. Alpine populations flower in February and March.

SPECIMENS EXAMINED: *A. P. Druce*, Hare Creek, Upper Wairau, CHR 401232; *D. Glenny* 6750, Fenella Hut, CHR 559321; *D. Glenny* 6777, 6824b, Cobb Valley, 530458, 541820; *D. Glenny* 6282 Clarence Valley, CHR 509800; *M. J. A. Simpson* 6871, Mt Robert, CHR 227750; *M. J. A. Simpson* 3084, Travers Range, CHR 120774.

CONSERVATION STATUS: Abundant in the Cobb Valley and on the St Arnaud and Travers ranges, not threatened.

ETYMOLOGY: *Patula* means "spreading", referring presumably to the often much branched caudex and multiple rosettes of large specimens.

ILLUSTRATIONS: Malcolm & Malcolm (1988, p. 107); Mark & Adams (1973, plate 74, upper right). The specimen illustrated is *A. F. Mark & N. M. Adams*, Cobb Valley, OTA 28016.

DISCUSSION: I have chosen a Kirk specimen from near Rotoiti as the lectotype. Both syntypes at WELT match the protologue. One, *J. B. Armstrong*, Canterbury Alps, is a specimen of *G. serotina*, and if taken as a lectotype, would make *G. serotina* a synonym of *G. patula*. The other, from Rotoiti, is this species, and agrees with common use of the name *G. patula*, which has often been applied to Nelson Lakes specimens.

G. patula is a difficult species to characterise, as there are no uniformly present qualitative differences from *G. montana*, although it differs in its smaller plant and flower size, but is more branched and with a larger number of flowers than *G. montana*. These size and number differences are ones that can be taken in by the eye, making it relatively easy to recognise the species. There is a gap in the species' distribution between the Cobb Valley and Nelson Lakes. This gap is occupied by a robust form of *G. montana*. Herbarium specimens indicate the two species grow very near to each other at Lake Sylvester.

Gentianella saxosa (G.Forst.) Holub, *Folia Geobot. Phytotax.* 3: 218 (1968).

Basionym: *Gentiana saxosa* G.Forst., *Kongl. Vetensk. Acad. Handl.* 38: 184, t.5 (1777).

Holotype: *G. Forster*, Dusky Sound, BM. Isotypes: B-W, K.

≡ *Oreophylax saxosus* (G. Forst.) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

≡ *Chionogentias saxosa* (G.Forst.) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).
= *Gentiana saxosa* var. *recurvata* Kirk, *Trans. & Proc. New Zealand Inst.* 17: 224
(1885). Holotype: *T. Kirk*, Dog Island, 18 January 1884, WELT 47548!
= *Gentiana hookeri* J.B.Armstrong, *Trans. & Proc. New Zealand Inst.* 13: 335–343
(1881) pro parte. Syntype: *Rev. Mr Stack*, Stewart Island, CHR! ex Christchurch
Botanic Gardens, 6302.

DESCRIPTION: Plants polycarpic, height in flower 40–170 mm. Flowering stems terminal and lateral or lateral only, (2–)4–16 per plant, stems tinted purple-black, lateral flowering stems decumbent, 1.3–2.6 mm diameter when dry, flowering stem leaves 4–5 pairs per stem, lowest pedicels from halfway up flowering stem. Rosette leaves narrowly elliptic to elliptic, leaf apex rounded, 17.8–87 mm long, 3.2–17.5 mm wide, green, not recurved; petiole distinct, 14.5–64 mm long, 0.7–3.4 mm wide at leaf base. Pedicels 1 per axil, 10–67 mm long, 1.4–1.5 mm diameter, 0.7–1.3 mm diameter when dry. Flowers 9–82 per plant, 15.0–24.2 mm long. Calyx 6.8–8.8 mm long, green; lobes 4.5–6.2 mm long, 2.0–3.2 mm wide at base, distinctly recurved, apices acute, margins minutely serrulate, sinus hairs absent. Corolla 13.7–15.7 mm long, white, veins uncoloured; tube 3.5–4.0 mm long; lobes 9.6–11.2 mm long, 6.7–7.4 mm wide; nectaries 2.5–3.7 mm from corolla base. Filaments 7.6–8.1 mm long from corolla base, 0.7–0.8 mm wide. Anthers 2.0–2.1 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules 30–44 per ovary. Capsule 10.0–19.3 mm long. FL. late Jan–early Feb.

DISTRIBUTION: OTAGO: False Inlet. SOUTHLAND: Curio Bay, Orepuki, Waituna Lagoon, Bluff Hill, Oreti, Resolution Is., Breaksea Is., West Cape, Dusky Sound. STEWART ISLAND: Big Bungaree Beach, Mason Bay, Ruggedy Beach, Muttonbird Islands, Big South Cape Is., Codfish Is., Green Is.

HABITAT: Coastal rock outcrops, coastal turflands, sand dunes; 0–150 m.

CHROMOSOME NUMBER: $n = 18$ (Post 1983).

RECOGNITION: By its coastal habitat, which is shared on the New Zealand mainland only with *G. lineata* and *G. scopulorum*. *G. saxosa* has larger flowers (15–25 mm long, cf. c. 10 mm long) and wider, recurved calyx lobes (2.0–3.2 mm wide, cf. 1.1–1.7 mm wide in

G. lineata).

VARIATION: The leaves vary considerably in the shape and size of the lamina and length of the petiole. Specimens from Stewart Island and its offshore islands have the largest leaves and this appears to be a constant genetic difference from other populations.

SPECIMENS EXAMINED: *D. Glenny* 6372, Big Bungaree Beach, CHR 509898; *B. Rance* 2/98, Waipapa Point, CHR 526415; *I. M. Ritchie*, Betsy Island, Muttonbird Islands, CHR 410445.

CONSERVATION STATUS: A widespread and common species and not threatened in most parts of its range.

ETYMOLOGY: *Saxosa* means 'of rocky places'.

ILLUSTRATIONS: Johnson (1997, p. 147); Metcalf (1993, plate 92); Moore & Irwin (1978, p. 147, fig. 2); Wilson (1982, p. 248).

DISCUSSION: Kirk's var. *recurvata* from Dog Island is not recognised as its distinguishing feature, the recurved calyx lobes, are a constant feature of *G. saxosa*.

Gentianella scopulorum Glenny sp. nov.

DIAGNOSIS: Ab *Gentianellae saxosae* differt in folia orbicular, non ellipticus; veno corollae purpureo; lobi calycæ planæ; caule floribus carmesinus, antherae brevior, 1.0–1.6 mm longæ.

HOLOTYPE: *W. Townson* 504, Rocks near the sea at Charlestown, south of Westport, AK 7316! upper plant on sheet. Isotype: AK 7317!

DESCRIPTION: Plants polycarpic, height in flower 70–130 mm. Flowering stems terminal and lateral, 4–10 per plant, stems tinted crimson, 1.4–2.3 mm diameter when dry. Rosette leaves orbicular, 35–44 mm long, 10.0–17.5 mm wide, green, not recurved, margin not thickened; apex rounded; petiole distinct, 19–30 mm long, 1.4–2.2 mm wide. Pedicels 1 per leaf axil, 1–16 mm long, 0.9–1.3 mm diameter when fresh, 0.5–0.8 mm

diameter when dry. Flowers 8–38 per plant, 12–15 mm long, rarely female. Calyx 6.0–8.2 mm long, green, hairs at calyx–corolla fusion line present; lobes 3.9–5.5 mm long, 1.8–2.4 mm wide, plane, sinus hairs absent, sparse or abundant. Corolla 9.5–14.8 mm long, veins coloured; tube 2.6–4.5 mm long; lobes 9.6–10.5 mm long, 3.3–5.0 mm wide; nectaries 0.7–1.2 mm from corolla base. Filaments 5.0–7.4 mm long from corolla base, 0.6–0.8 mm wide. Anthers 1.0–1.5 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules 16–30 per ovary. Capsule 10.0–11.8 mm long. FL. Dec.

DISTRIBUTION: WESTLAND: Charleston, promontory south of Doctors Bay.

HABITAT: Coastal granite rock outcrops, among grasses, *Selliera radicans* turfland, with *Samolus repens*, *Brachyglottis traversii*, *Oreobolus strictus*, and in flaxland of *Phormium cookianum*, *Cortaderia richardii*, and *Isolepis*, c. 50 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: By its coastal habitat, purple corolla veins, short pedicels, and orbicular leaves. It is the only member of the *G. saxosa* group of species in which calyx sinus hairs are sometimes present. It is most similar to *G. saxosa*, and the two are compared in Table 10.

VARIATION: Insufficient material available to assess this.

SPECIMENS EXAMINED: *P. J. de Lange 1471* & *D. Norton*, Charleston, CHR 479209; *D. Glenny 6326*, Charleston, CHR 509848.

CONSERVATION STATUS: "Nationally critical" in the classification of Molloy et al. (2001). Known from only one locality, where only 36 plants were found in a careful search in 2001 (R. McLellan, pers. comm.). The population is threatened by trampling by rock-climbers, growth of weeds, and possibly by goat browsing. It is the most threatened gentian species in New Zealand. Recent attempts by the Department of Conservation to increase the numbers by *ex situ* cultivation have been successful (P. Knightbridge, pers. comm. 2002).

ETYMOLOGY: Scopulorum means "of cliffs", referring to the habitat.

ILLUSTRATIONS: None.

DISCUSSION: First collected at the Charleston site by W. Townson. A second population was recorded by Cheeseman (1925, p. 734) near Hokitika, based on a collection of *Helms*, but this specimen does not appear to be in AK.

Gentianella serotina (Cockayne) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 64 (1993).

Basionym: *Gentiana serotina* Cockayne, *Trans. & Proc. New Zealand Inst.* 47: 112 (1915). Holotype: *L. Cockayne*, Canterbury, Springfield, WELT 4724! Probable isotypes are: *L. Cockayne* 6 April 1899, label in Cockayne's handwriting: "No. 4283 *Gentiana* sp. Growing on stony ground in full sunshine – upper Canterbury Plain nr. Springfield, 660 m.", ex herb. Cheeseman, AK 7240!; *L. Cockayne*, April 1899, Upper Canterbury Plains, ex herb. H. B. Matthews, AK 209538!

≡ *Oreophylax serotinus* (Cockayne) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

≡ *Chionogentias serotina* (Cockayne) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

DESCRIPTION: Plants polycarpic, height in flower (80–)120–180(–300) mm. Caudex unbranched or branched, 10–35(–100) mm long, shaggy with dead leaf bases. Root 2.0–6.7 mm diameter at stem base. Flowering stems lateral only, or terminal on rosette-bearing branches, (1–)2–5–7(–13) per plant, largest flowering stem 1.9–3.0 mm diameter at base, 1.0–2.0 mm diameter when dry, stem colour green or tinted crimson or purple-black, lateral flowering stems erect or decumbent, flowering stem leaves 1–5 pairs per stem, lowest pedicels from near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves linear to narrowly elliptic, (32–)45–70–112(–160) mm long, (3.5–)4.0–9.4–13(–15) mm wide, green or tinted crimson or purple-black below and on petiole and veins, sometimes leaf surface speckled purple-black, V-shaped in section or channelled, recurved or not, apex acute, petiole absent to distinct, 15–40 mm long, (1.1–)1.5–2.2–3.7(–4.0) mm wide at leaf base. Flowering stem leaves narrowly elliptic, sessile. Flowers 1–14–20(–130) per plant, 15–21 mm long. Pedicels 1 or 2 per leaf axil, 12–26 mm long, 0.8–1.4 mm diameter, 0.5–1.0 mm diameter when dry. Calyx (7.4–)7.9–9.4–13.8 mm long, green or green tinted purple-black, hairs at calyx-corolla fusion line absent or present; lobes

4.6–6.3–9.7 mm long, (2.0–)2.1–2.6(–3.0) mm wide at base, plane, apices acute, margins smooth to serrulate, sinus hairs sparse, rarely abundant. Corolla 14.1–16.2–19.5 mm long, white, veins uncoloured; tube 4.3–6.2 mm long; lobes 9.6–13 mm long, 5.6–9.5 mm wide, hairs below sinus present; nectary (0.3–)0.5–1.9(–2.2) mm from corolla base. Filaments 7.0–9.8(–11.2) mm long from corolla base, (0.65–)0.8–1.0–1.1(–1.4) mm wide. Anthers (1.8–)2.0–2.3–3.0(–3.2) mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules (15–)22–41–57(–64) per ovary. Capsule 13–22 mm long. FL. Feb–Apr.

DISTRIBUTION (Fig. 70): CANTERBURY: Lees Valley, Banks Peninsula, Waimakariri Basin, Rakaia Basin, upper Canterbury Plains, Mt Potts, Heron Basin, Irishmans Creek, Mt Cook, Hunter Hills. OTAGO: Mt Ida, Mt Alta, Middlemarch, Maungatua. SOUTHLAND: Blue Mountain, Thomson Mountains, Livingstone Mountains, Eyre Mountains, Garvie Mountains, Hector Mountains (Tennants Peak), Mid Dome, Takitimu Mountains (including Tower Peak and Excelsior Peak).

HABITAT: Montane tall and short tussocklands and shrub tussocklands of *Festuca novae-zelandiae*, *Chionochloa macra*, *C. rigida*, and *C. flavescentis*, on river terraces, valley floors, less often on hillslopes and ridges, in well drained soils; with *Hebe odora*, *Dracophyllum rosmarinifolium*, *D. acerosum*, *Discaria toumatou*, *Coprosma* sp. aff. *parviflora*, *Pteridium esculentum*, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Poa colensoi*, *Aciphylla aurea*, *Oreomyrrhis ramosa*, and *Hypochoeris radicata*; 450–1675 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980); $n = 18$ (Post 1983).

RECOGNITION: Close to *G. bellidifolia*, both species being polycarpic and sharing lateral-only flowering stems. *G. serotina* usually has longer, narrower, flatter leaves than most specimens of *G. bellidifolia*. The plants are usually taller, and often have more flowering stems and flowers per plant. The flowering stems tend to be decumbent while Otago and Southland plants of *G. bellidifolia* tend to be erect from the base. The two are compared in Table 39. *G. serotina* resembles *G. corymbifera* subsp. *gracilis* in its thin black stems and grows in the same habitat (valley floor grasslands on well drained soils), but differs in being polycarpic rather than biennial, in having only lateral flowering stems (they are always terminal in *G. corymbifera*), and in having thinner

flowering stems (2.8–3.0 mm diameter, not 4.2–5.3 mm).

SPECIMENS EXAMINED: *A. P. Druce* 1567, Oreti Valley, CHR 472159; *D. Glenny* 6381, Garvie Mountains, CHR 509907; *D. Glenny* 6429, Lake Lyndon, CHR 509956; *D. Glenny* 6906, Lake Lyndon, CHR 530579; *C. Jensen*, Lammermoor Range, CHR 526408; *P. N. Johnson* 1362, West Dome, CHR 511792; *B. D. Rance*, Helen Peaks, Eyre Mountains, CHR 516252; *G. Simpson*, Maungatua, CHR 109508; *N. Simpson*, Rock & Pillar Range, CHR 472159; *L. R. Stemmer*, Lees Valley, CHR 259206.

CONSERVATION STATUS: Widespread and common.

ETYMOLOGY: *Serotina* means "late-coming", referring to the late flowering, especially if compared with *G. corymbifera*, which flowers in January in the same habitat.

ILLUSTRATIONS: None.

DISCUSSION: In Canterbury, *G. serotina* is well separated in habitat and morphology from *G. bellidifolia*, but on mountains of Otago and Southland, particularly the Rock and Pillar and Old Man ranges, and the southern Hector Mountains, *G. bellidifolia* is tall and sometimes has long and narrow leaves, making the two species very difficult to distinguish. There appear to be no reliable characters to separate the two in all cases, and this casts some doubt on their distinctness as species in this region.

Gentianella spenceri (Kirk) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 65 (1993).

Basionym: *Gentiana spenceri* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 335 (1895).

Holotype: *Rev. F. H. Spencer*, Mount Rochfort, near Westport, 2000ft, Jan 1880, WELT 4711!

≡ *Chionogentias spenceri* (Kirk) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

DESCRIPTION: Plants monocarpic, biennial, height in flower (85–)100–170–270 mm. Caudex unbranched, 20–100 mm long, stolons absent. Root 2.0–3.1 mm diameter at stem base. Flowering stems terminal and lateral, 1–7 per plant, largest flowering stem 2.0–3.3 mm diameter at base, 1.9–2.7 mm diameter when dry, green or tinted crimson, lateral flowering stems erect, flowering stem leaves 1–3 pairs per stem, lowest pedicels

from near base of flowering stem or halfway up flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves elliptic, orbicular, obovate, or ovate, 25–44–80(–93) mm long, 13.0–17.5–22 mm wide, green or tinted crimson below or tinted purple-black, flat or with petiole V-shaped, sometimes very shallowly 2- or 3-lobed, sometimes recurved at the apex, leaf apex usually rounded, occasionally acute or retuse, petiole absent to distinct, 15–53 mm long, 2.0–5.8 mm wide at leaf base. Flowering stem leaves orbicular with shorter petioles than rosette leaves or sessile. Pedicels 1 or 2 per leaf axil, 1.5–10 mm long, 1.0–1.2 mm diameter, 0.37–0.7 mm diameter when dry. Flowers 3–18–33 per plant, 9.0–10.5–16 mm long. Calyx 6.0–8.8–11.0 mm long, green, hairs at calyx-corolla fusion line absent or present; lobes 5.3–9.3 mm long, 1.4–2.1 mm wide at base, plane, apices acute, margins smooth or minutely serrulate, sinus hairs absent or sparse. Corolla 9.3–14 mm long, white, sometimes tinted on outside of corolla lobes, veins usually coloured purple or crimson, rarely uncoloured; tube 2.5–4.1 mm long; lobes 5.4–9.9 mm long, 3.2–4.4 mm wide, hairs below sinus absent or present; nectary 0.8–2.0 mm from corolla base. Filaments 5.9–8.0 mm long from corolla base, 0.6–0.7 mm wide. Anthers 1.1–1.3 mm long, anther wall dark red, mouth orange-red, extrorse at anthesis, pollen dull pink. Stigma crimson. Ovules (4–)22–33 per ovary. Capsules 6.2–12.0 mm long. FL. (Dec–)Jan–Feb(–Mar).

DISTRIBUTION (Fig. 71): NELSON: Takaka Hills, Haupiri Range, Heaphy, Cobb Valley, Hope Range, Anatoki Range, Glasgow Range. WESTLAND: Brunner Range, Paparoa Range, Hohonu Range, Tuhua Range, Arahura River, Mungo River, Whitcombe River.

HABITAT: Subalpine forest, clearings in such forest, or under scrub, often on ridges, under forest of *Nothofagus solandri* var. *cliffortioides*, *N. menziesii*, *Dracophyllum traversii*, *Metrosideros umbellata*, *Weinmannia racemosa*, *Libocedrus bidwillii*, *Lagarostrobos colensoi*, *Phyllocladus alpinus*, *Griselinia littoralis*, *Pseudopanax lineare*, *Dracophyllum rosmarinifolium*, often with an understorey of *Archeria traversii*, *Coprosma foetidissima*, and *Myrsine divaricata*; with *Phormium cookianum*, *Gahnia pauciflora*, *Gaultheria crassa*, *Exocarpus bidwillii*, *Cyathodes empetrifolia*, *Empodisma minus*, *Gleichenia dicarpa*, *Libertia pulchella*, *Uncinia filiforme*, *Luzuriaga parviflora*, *Astelia nervosa*, *Blechnum procerum*, *Lycopodium scariosum*, *Hymenophyllum multifidum*, *Dicranoloma robustum*, *Leucobryum candidum*, *Ptychomnion aciculare*, *Wijkia extenuata*, *Acromastigum anisostomum*, *Racomitrium pruinosum*, *Cladia sullivanii*, and *C. corallina*. Sometimes epiphytic in cracks of tree trunks;

(300–)650–1500 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: Characteristic of *G. spenceri* are its orbicular leaves with apex rounded, and often with a very slight lobing of the leaf, the unbranched caudex with a single basal rosette of leaves, the short pedicels (1.5–10 mm long), the few pairs of flowering stem leaves (1–3 pairs), the smaller late flowers arising from low on the plant, the pandurate calyx lobes, and the purple corolla veins. It is one of only three forest taxa, the others being *G. chathamica* subsp. *nemorosa* of the North Island, and *G. tenuifolia*. *G. spenceri* is a species of higher altitudes than *G. tenuifolia*. *G. spenceri* is not as tall as *G. tenuifolia* (40–270 mm tall, not 230–530 mm tall), it has shorter orbicular leaves with a rounded apex rather than elliptic leaves with acute apices. *G. spenceri* and *G. chathamica* subsp. *nemorosa* share purple corolla veins, an unbranched caudex, and a petiolate leaf, but *G. spenceri* has fewer flowering stems. Purple corolla veins are shared with several other species in Nelson and Westland: *G. tenuifolia*, sometimes *G. patula*, and sometimes *G. montana* var. *stolonifera*. The rosette leaves of *G. spenceri* can sometimes resemble those of *G. montana* but that species differs in being found in more open habitat, the pedicels are longer, the plants are perennial and often have a branched caudex, and its flowers are larger.

VARIATION: Populations in the Heaphy area of Nelson have flowering stem leaves that are petiolate, whereas they are sessile on plants from all other areas. Westland plants have larger leaves (Fig. 18).

SPECIMENS EXAMINED: *D. Glenny* 6440, Buckland Peaks, CHR 509967; *D. Glenny* 6756, Cobb Valley, CHR 530439; *D. Glenny* 6810, Perry Saddle, CHR 530484; *D. Glenny* 7363, Granity Pass, CHR 559989; *G. Jane*, Mt Stevens, CHR 526405.

CONSERVATION STATUS: The species has a wide distribution from western Nelson to central Westland and is not uncommon there, and is not in a threatened habitat.

ETYMOLOGY: Named for F. H. Spencer (1854–1932), New Zealand-born amateur botanist and curate at Collingwood in 1880 at the time of his collecting trip to Denniston Plateau (Godley 1992).

ILLUSTRATIONS: Cheeseman (1914, vol. 2, plate 141); Kirk (1895, plate 27a); Salmon (1991, p. 241, plate 1002). Mark & Adams (1973, plate 75 right side) does not show this species, but possibly *G. montana*.

DISCUSSION: A distinctive species in Nelson and most closely related to *G. tenuifolia*. Some specimens are difficult to assign to one or the other of these two species. They appear to be allopatric but almost meet in the Cobb Valley and could be sympatric in some other nearby valleys. The southern limit of *G. spenceri* appears to be in Central Westland in the Whitcombe Valley at Cataract Creek (*P. Bellingham* 965, CHR 530226). In the valleys of Central Westland, *G. tenuifolia* also appears to be present, and their distribution may overlap there.

Gentianella stellata Glenney, sp. nov.

DIAGNOSIS: *Gentianellae tenuifoliae* affinis et similis, sed corolla alba, foliis crassis, coriaceis atque politis, rosulatis, recurvis, petiolo absens, foliis 4.3–5.7 mm lato ad basis, lobis calycis recurvis, lobis calycis latoribus 1.6–3.0 mm latis, nectario ex base corollae longius insidenti, 1.7–2.7 mm, ciliis in sinibus calycinis sparsis differt.

HOLOTYPE: A. P. Druce, mineral belt, south end of D'Urville Island, 1200 ft, shrubland, April 1981, CHR 387194! plant on upper left of sheet (Fig. 72).

= *Gentiana pleurogynoides* var. *umbellata* Kirk, *Trans. & Proc. New Zealand Inst.* 27: 335 (1895) pro parte. Lectotype (here chosen): H. B. Kirk, D'Urville Island, Nov 27 1889, WELT 47786! large plant on left of sheet.

DESCRIPTION: Plants monocarpic, biennial, height in flower 180–290–730 mm. Caudex unbranched or branched with branches short, c. 30 mm long. Root 1.8–6.0 mm diameter at stem base. Flowering stems terminal only or terminal and lateral, 1–6 per plant, largest flowering stem 1.7–3.4–5.4 mm diameter at base, stem colour green or tinted crimson, purple-black, or bronze, lateral flowering stems erect when present, flowering stem leaves 3–6 pairs per stem, lowest pedicels from near base of flowering stem or halfway up flowering stem or near apex of flowering stem. Rosette of leaves present and distinct from flowering stem leaves, leaves narrowly elliptic or elliptic, 12–55–100 mm long, (3.7–)6.0–8.7–19 mm wide, green or tinted crimson, purple-black, or bronze,

flat or slightly to strongly channelled, recurved; leaf apex acute or rounded; petiole absent, leaf 2.9–4.2–5.7 mm wide at base. Flowering stem leaves similar to rosette leaves but smaller, ovate, strongly recurved and channelled. Pedicels 1 or 2 per leaf axil, 3–45 mm long (those from low on the flowering stem very long), 0.75–1.5 mm diameter, 0.6–1.0 mm diameter when dry. Flowers 11–38(–59) per plant, 14–29 mm long. Calyx 6.0–9.7–13 mm long, green or crimson, hairs at calyx-corolla fusion line absent or present; lobes 3.8–7.0–8.2 mm long, 1.5–3.0 mm wide at base, recurved, apices acute, margins smooth or minutely serrulate, sinus hairs few. Corolla (10–)13–17–23 mm long, white, veins uncoloured; tube 3.0–6.3 mm long; lobes 11.5–19 mm long, 6.3–9.5 mm wide, hairs below sinus few or absent; nectary 1.7–2.7 mm from corolla base. Filaments 5.9–10.6 mm long from corolla base, 0.6–1.2 mm wide. Anthers 1.7–2.2–3.1 mm long, anther wall yellow or blue-black, mouth yellow, extrorse at anthesis. Stigma colourless or slightly tinted blue. Ovules 18–43–68 per ovary, ovary turning purple in maturity. Capsule 11.5–21 mm long. FL. Mar–Apr(–Aug).

DISTRIBUTION (Fig. 71): NELSON: D'Urville Island, Bryant Range, Dun Mountain, Mt Starveall, Red Hills (Richmond Range).

HABITAT: Montane *Leptospermum scoparium* and *Lepidosperma australe* shrubland and scrub on ultramafic soils, with *Dracophyllum longifolium*, *Phormium cookianum*, *Poa colensoi*, *Anaphalioides bellidioides*, and *Racomitrium pruinosum*; *Chionochloa defracta* tussockland on ultramafic soils; *C. rubra* tussockland on peat soils, with *Carex sinclairii* and *Schoenus pauciflorus*; 180–900 m.

CHROMOSOME NUMBER: Unknown.

RECOGNITION: A tall species with a central flowering stem and unbranched caudex, with large white flowers and yellow anthers. The leaves are recurved and strongly channelled, thick in texture, as are the flowering stem leaves. Closest to *G. tenuifolia* but amply distinct from that species (Table 26).

VARIATION: A relatively uniform species.

SPECIMENS EXAMINED: A. P. Druce, D'Urville Island, CHR 387194; D. Glenny 6436, Right Branch Motueka River, CHR 509963; P. Heenan, Right Branch Motueka River,

CHR 565234; *G. Jane*, Hackett Valley, CHR 526439; *G. Jane*, Dew Lakes, CHR 516236.

CONSERVATION STATUS: Confined to ultramafic areas in Nelson but abundant there and not threatened.

ETYMOLOGY: 'Stellata' refers to the star-shaped corolla as the corolla lobes recurve more strongly than in other species.

DISCUSSION: In cultivation this species becomes more similar to *G. tenuifolia* but lacks the broadly elliptic leaves of that species, and keeps the leaf texture and recurving of the leaves and the differences in flower colour and shape.

Gentianella tenuifolia (Petrie) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 65 (1993).

Basionym: *Gentiana tenuifolia* Petrie, *Trans. & Proc. New Zealand Inst.* 45: 270 (1913).

Holotype: *W. Townson*, near Lyell, S. W. Nelson, WELT 4721! with the note "Robust large leaved form".

≡ *Chionogentias tenuifolia* (Petrie) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

DESCRIPTION: Plants monocarpic, biennial, height in flower 230–330–530 mm. Caudex unbranched, 7–65 mm long. Root 2.1–7.0 mm diameter at stem base. Flowering stems terminal only or terminal and lateral, 1–8 per plant, largest flowering stem 1.6–3.9 mm diameter at base, central flowering stem more robust than the laterals, stem colour green or tinted crimson, lateral flowering stems erect or decumbent, flowering stem leaves 4–6 pairs per stem, lowest pedicels from near base of flowering stem or halfway up flowering stem. Rosette of leaves distinct from flowering stem leaves, leaves narrowly elliptic or elliptic, 40–72–102(–117) mm long, 8.5–15–20(–24) mm wide, green or tinted crimson below, flat, not recurved, thin in texture, matt on adaxial leaf surface, with lateral veins projecting from the abaxial leaf surface, leaf apex acute; petiole absent to indistinct, (20–)30–33 mm long, 3.0–4.8 mm wide at leaf base. Flowering stem leaves ovate, apices acute. Pedicels 1 or 2 per leaf axil, 4–30 mm long, 0.7–1 mm diameter, 0.4–0.6 mm diameter when dry. Flowers 13–85 per plant, 11.2–16 mm long. Calyx 6.0–9.8 mm long, green, hairs at calyx-corolla fusion line present; lobes 4.0–5.9 mm long, 1.4–2.0 mm wide at base, plane or recurved, apices acute, margins smooth or

minutely serrulate, sinus hairs absent. Corolla 9.8–12–17.2 mm long, white, veins usually purple, rarely colourless; tube 3.0–3.2 mm long; lobes 6.6–12.2 mm long, 3.2–5.0 mm wide, hairs below sinus present; nectary 0–1.0 mm from corolla base. Filaments 6.5–7.9 mm long from corolla base, 0.5–0.8 mm wide. Anthers 1.3–1.8–2.1 mm long, anther wall blue-black, mouth yellow or orange-red, extrorse or horizontal at anthesis. Stigma crimson or blue. Ovules 18–33–53 per ovary. Capsule 9.5–17 mm long. FL. Jan–Feb(–Apr).

DISTRIBUTION (Fig. 73): NELSON: Cobb Valley, Takaka Ridge, Pikikuruna Range, Rotoiti, D’Urville Island, Wooded Peak, Richmond Range, Lyell Range.

MARLBOROUGH: Leatham River, Haldon Hills, Mt Tapuaeunuku, Hapuku River.

CANTERBURY: Lake Sumner, Kowai Bush, Craigieburn Range, Cass. WESTLAND: Toaroa, Arahura, Styx, and Wanganui rivers.

HABITAT: Montane *Nothofagus* forest and dry scrub margins, with *Kunzea ericoides*, *Coprosma linariifolia*, *Cyathodes juniperina*, *Gaultheria crassa*, *G. macrostigma*, *Helichrysum filicaule*, *Hypochoeris radicata*, *Blechnum penna-marina*, and *Lycopodium volubile*; 500–1260 m. Usually on well drained soils. On ultramafic soils in the Cobb Valley but replaced by *G. stellata* on ultramafic soils on the Red Hills of the Richmond Range.

CHROMOSOME NUMBER: $n = 18$ (Post 1983).

RECOGNITION: By its monocarpy, the tall robust terminal flowering stem (and many thinner lateral flowering stems in larger specimens), the short pedicels in the terminal corymb, the large, flat, thin-textured leaves, in which the veins project from the underleaf surface, by the crimson to purple tint that is common in the leaves, flowering stems, stigma, and corolla veins. Shares with *G. spenceri* crimson coloration in the leaves and flowers, a central stout flowering stem, and usually five or fewer lateral stems from the basal rosette, the flowers are small, on thin short pedicels, and the flowers are abundant from stem leaf axils even near the flowering stem base. The two species differ in size, *G. tenuifolia* being taller. *G. tenuifolia* has elliptic leaves while *G. spenceri* has spatulate leaves, and *G. tenuifolia* has ovate to narrowly elliptic flowering stem leaves while *G. spenceri* has orbicular stem leaves (Table 25, Fig. 18). *G. tenuifolia* is also similar to *G. stellata* and they are compared in Table 26.

VARIATION: In Central Westland in the Toaroha, Arahura, Styx, and Wanganui rivers there are plants with robust flowering stems, large leaves that are thin in texture and have the main lateral veins projecting on the lower leaf surface. They lack the purple corolla veins and purple stigmas seen in plants in the rest of the species' distribution. Such plants are found in clearings in *Olearia ilicifolia* forest and *Podocarpus hallii* forest, and appear to belong to this species, but better collections may show otherwise.

SPECIMENS EXAMINED: *P. Bellingham*, Hapuku River, CHR 526395; *S. P. Courtney*, Flora Saddle, CHR 516225; *D. Glenny* 6776, Red Hills, CHR 530457; *D. Glenny* 6824, Cobb Valley, CHR 530498; *D. Glenny* 6930, Harman Hut; *P. Wardle* 94/71 & *R. P. Buxton*, Wanganui River, CHR 508458; *P. Wardle*, Smythe River; *P. Wardle*, *R. P. Buxton* & *K. A. Ford*, Wilberg Range, CHR 500108.

CONSERVATION STATUS: A widespread and common species.

ETYMOLOGY: *Tenuifolia* refers to the thin texture of the leaves.

ILLUSTRATIONS: Fig. 74; Malcolm & Malcolm (1988, p. 107); Salmon (1991, p. 241, plate 1003).

DISCUSSION: This is a distinct species with a southern limit in mid-Canterbury. Its affinities are with *G. stellata* (see there for comparison) and *G. spenceri*. *G. tenuifolia* and *G. spenceri* are nearly sympatric in the Cobb Valley and may be sympatric in Central Westland. They share a habitat preference for well lit forest or forest margins or scrub, but *G. spenceri* is subalpine while *G. tenuifolia* is montane.

Gentianella vernicosa (Cheeseman) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 65 (1993).

Basionym: *Gentiana vernicosa* Cheeseman, *Man. New Zealand fl.* 1145 (1906).

Lectotype (here chosen): *F. G. Gibbs*, Nelson, Mt Lockett, 4000 ft, March 1903, AK 7269!, the single plant on the sheet. Annotation on 7269 says: "Type selected: December 1941, L. M. Cranwell". Isolectotype: AK 209540!

≡ *Oreophylax vernicosus* (Cheeseman) Á.Löve, *Taxon* 32: 511 (1983), nom. inval.

≡ *Chionogentias vernicosa* (Cheeseman) L.G.Adams, *Austral. Syst. Bot.* 8: 978 (1995).

= *Gentiana gracilifolia* Cheeseman, *Man. New Zealand fl.* 1144 (1906). Syn. nov.

Lectotype (here chosen): *F. G. Gibbs*, Tarns on Mt Arthur Plateau, Nelson, alt 4000 ft, Jan 1905 AK 7209! plant on lower left of sheet. Annotated "Type selected: Dec 1941 designated by L. M. C." Isolectotype: WELT 47696!

≡ *Chionogentias gracilifolia* (Cheeseman) L.G.Adams, *Austral. Syst. Bot.* 8: 977 (1995).

≡ *Gentianella gracilifolia* (Cheeseman) T.N.Ho & S.W.Liu, *Bull. Brit. Mus. (Nat. Hist.), Bot.* 23: 62 (1993).

DESCRIPTION: Plants polycarpic, rarely monocarpic and biennial, height in flower 80–110–290 mm. Caudex unbranched or branched, 35–120 mm long. Stolons arising from branched caudex occasionally present. Root 1.2–2.0 mm diameter at stem base. Flowering stems terminal on main caudex or its branches, 1–16 per plant, largest flowering stem 1.0–2.5 mm diameter at base, 0.9–2.0 mm diameter when dry, stems tinted purple-black, rarely green, erect or decumbent, flowering stem leaves 3–5 pairs per stem, lowest pedicels from near apex of flowering stem, flowers often solitary on a stem. Rosettes of leaves present but grading to flowering stem leaves, leaves narrowly elliptic, glossy, thick in texture without projecting veins, (12.0–)14.5–19–25(–31) mm long, (1.8–)2.4–3.8–5.7(–6.0) mm wide, green, rarely tinted crimson below, flat or slightly V-shaped in section, not recurved, apex acute, petiole absent, leaf 1.0–2.2–3.4 mm wide at leaf base. Flowering stem leaves narrowly ovate. Pedicels 1 or 2 per leaf axil, 2–15–27 mm long, 0.9–1.4 mm diameter, 0.5–0.65 mm diameter when dry. Flowers 1–5–24 per plant, 13.0–18.3 mm long. Calyx 6.8–8.3–10.8 mm long, green or tinted purple-black or brown, hairs at calyx-corolla fusion line present; lobes 4.1–8.1 mm long, 1.9–3.2 mm wide at base, plane, apices acute, margins smooth, sinus hairs absent, sparse, or abundant. Corolla (10.9–)13.6–16.0–16.8 mm long, white, veins uncoloured; tube 3.0–4.5 mm long, lobes 8.3–12.5 mm long, 7.0–10.9 mm wide, hairs below sinus present; nectary 0.3–0.6 mm from corolla base. Filaments 7.1–8.7–9.4 mm long from corolla base, 0.7–0.8–0.9 mm wide. Anthers 1.8–2.6–2.9 mm long, anther wall blue-black, mouth yellow, extrorse at anthesis. Stigma colourless. Ovules 28–47–64 per ovary, turning slightly blue in maturity. Capsule 13–18 mm long. FL. (Feb–)Apr.

DISTRIBUTION (Fig. 75): NELSON: Westhaven, Goulard Downs, Lead Hills, Anatoki, Cobb Valley, Mt Arthur Range, Stormy Ridge, Mt Owen, "Turks Cap Range", Matiri Range.

HABITAT: Alpine short tussocklands of *Chionochloa australis* and mosaics of *C. australis* and shorter *C. pallens* especially on or near ridges, with *Celmisia spectabilis*, *C. discolor*, *Brachyglottis bellidioides*, *Hebe macrantha*; less often in moist *Chionochloa rubra* tussocklands in alpine bogs or high altitude valley floors, often growing through *Sphagnum cristatum*, then with *Celmisia dallii*, *Hebe odora*, *Bulbinella hookeri*, *Dracophyllum prunum*, *Oreobolus pectinatus*, *Carpha alpina*, *Drosera arcturi*, *Epacris alpina*, *Lepidothamnus laxifolius*, and *Celmisia gracilentia*; 550–1500 m.

CHROMOSOME NUMBER: $2n = 36$ (Hair et al. 1980); $n = 18$ (Post 1983).

RECOGNITION: By the very narrowly elliptic leaves that lack a petiole, are thick, very glossy and green, and usually lacking in red or purple pigments, and by the multiple purple-black flowering stems with few flowers. Most similar to *G. montana* var. *stolonifera* but differs in having shorter leaves that are 12–19–31 mm long, not 29–34–39 mm long, and are narrower (1.8–3.8–6.0 mm wide, not 6.0–8.0–10.0 mm wide).

VARIATION: Variable in height, leaf length and width, but these differences mostly reflect the age of the plant and the soil fertility. However, there appears to be a wide-leaved form in the area directly north and east of the Cobb Valley, and the type of *G. vernicosa* is an example of this. Examples of this variant are *R. Mason*, Ridge between Anatoki and Douglas ranges, CHR 34918, and *A. P. Druce*, Hoary Head, CHR 395907.

SPECIMENS EXAMINED: *D. Glenny* 6752, Burgoo Saddle, CHR 530436; *D. Glenny* 6826, Mt Arthur, CHR 530500; *D. Glenny* 7367a, Sentinel Hill, CHR 559993; *D. Glenny* 7412, Garibaldi Ridge, CHR 560043; *D. Glenny* 7432, Cundy Creek, CHR 560061; *D. Glenny* 7445, Loveridge Peak, CHR 560073; *A. Wood*, "Turks Cap Range", CHR 526420.

CONSERVATION STATUS: Common throughout its range and not threatened.

ETYMOLOGY: *Vernicosa* means "varnished", referring to the glossy leaves.

ILLUSTRATIONS: Fig. 76; Cheeseman (1914, vol. 2, plate 137) labelled as *Gentiana gracilifolia*.

DISCUSSION: *G. vernicosa* and *G. gracilifolia* are one species, as pointed out by Druce (1974, p. 425). The names were published simultaneously, and I have retained *G. vernicosa*.

Incertae sedis

Gentiana hookeri J.B.Armstrong, *Trans. & Proc. New Zealand Inst.* 13: 340 (1881) pro parte. One of the two syntypes is *J. B. Armstrong*, "Canterbury and Otago Provincial Districts, common at considerable elevations". This specimen is not in the Armstrong Herbarium at CHR. The other syntype is a specimen of *G. saxosa* (see synonymy there).

Australian species of Gentianella

The Australian species placed by Adams (1995) in *Chionogentias* should be placed in *Gentianella* for the reasons given in the Introduction. To briefly recap, the New Zealand and Australian gentians (with the exclusion of four species of *Gentiana s. s.* (Adams 1996) belong in the same genus as most of the South American species. Segregation of these short-corolla-tubed species (sometimes termed the Southern gentians) should not be done until the relationships between species at the base of *Gentianella* are clear, if at all. A combination in *Gentianella* already exists for one species: *Gentianella diemensis* (Griseb.) J.H.Willis. For the remainder, new combinations are required in *Gentianella* for the Australian species and these are provided below. I have examined specimens representing all the species except for *G. grandis*, but not the types.

***Gentianella barringtonensis* (L.G.Adams) Glenny, comb. nov.**

BASIONYM: *Chionogentias barringtonensis* L.G.Adams, *Austral. Syst. Bot.* 8: 974 (1995).

***Gentianella bawbawensis* (L.G.Adams) Glenny, comb. nov.**

BASIONYM: *Chionogentias bawbawensis* L.G.Adams, *Austral. Syst. Bot.* 8: 961 (1995).

***Gentianella brevisepala* (L.G.Adams) Glenny, comb. nov.**

BASIONYM: *Chionogentias brevisepala* L.G.Adams, *Austral. Syst. Bot.* 8: 967 (1995).

***Gentianella clellandii* (L.G.Adams) Glenny, comb. nov.**

BASIONYM: *Chionogentias clellandii* L.G.Adams, *Austral. Syst. Bot.* 8: 968 (1995).

Gentianella cunninghamii (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias cunninghamii* L.G.Adams, *Austral. Syst. Bot.* 8: 962 (1995).

Gentianella cunninghamii subsp. *major* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias cunninghamii* subsp. *major* L.G.Adams, *Austral. Syst. Bot.* 8: 564 (1995).

Gentianella diemensis subsp. *plantaginea* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias diemensis* subsp. *plantaginea* L.G.Adams, *Austral. Syst. Bot.* 8: 954 (1995).

Gentianella eichleri (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias eichleri* L.G.Adams, *Austral. Syst. Bot.* 8: 973 (1995).

Gentianella grandis (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias grandis* L.G.Adams, *Austral. Syst. Bot.* 8: 960 (1995).

Gentianella gunniana (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias gunniana* L.G.Adams, *Austral. Syst. Bot.* 8: 969 (1995).

Gentianella muelleriana (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias muelleriana* L.G.Adams, *Austral. Syst. Bot.* 8: 955 (1995).

Gentianella muelleriana subsp. *alpestris* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias muelleriana* subsp. *alpestris* L.G.Adams, *Austral. Syst. Bot.* 8: 958 (1995).

Gentianella muelleriana subsp. *jingerensis* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias muelleriana* subsp. *jingerensis* L.G.Adams, *Austral. Syst. Bot.* 8: 957 (1995).

Gentianella muelleriana subsp. *willisiana* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias muelleriana* subsp. *willisiana* L.G.Adams, *Austral. Syst. Bot.* 8: 959 (1995).

Gentianella pleurogynoides (Griseb.) Glenný, comb. nov.

BASIONYM: *Gentiana pleurogynoides* Griseb., Gen. Sp. Gent. 236 (1838).

Gentianella pleurogynoides subsp. *milliganii* (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias pleurogynoides* subsp. *milliganii* L.G.Adams, *Austral. Syst. Bot.* 8: 967 (1995).

Gentianella polysperes (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias polysperes* L.G.Adams, *Austral. Syst. Bot.* 8: 970 (1995).

Gentianella sylvicola (L.G.Adams) Glenný, comb. nov.

BASIONYM: *Chionogentias sylvicola* L.G.Adams, *Austral. Syst. Bot.* 8: 972 (1995).

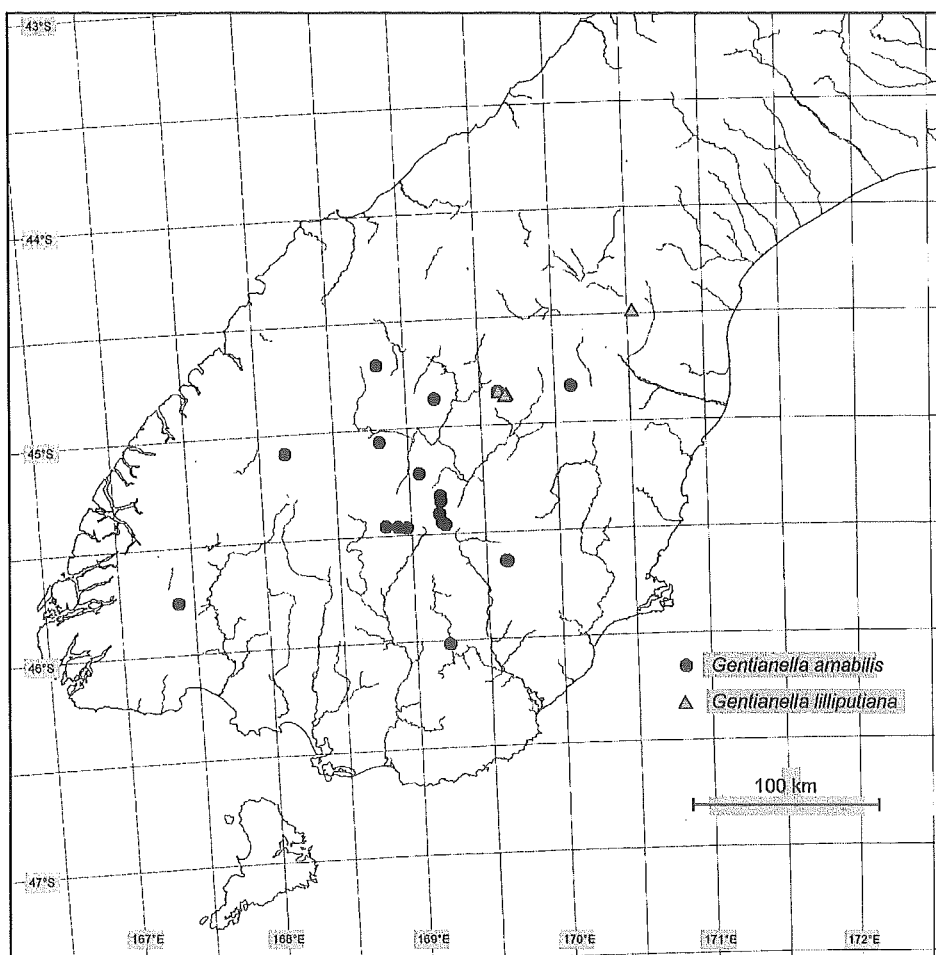


Fig. 47 Distribution of *Gentianella amabilis* and *G. lilliputiana*.

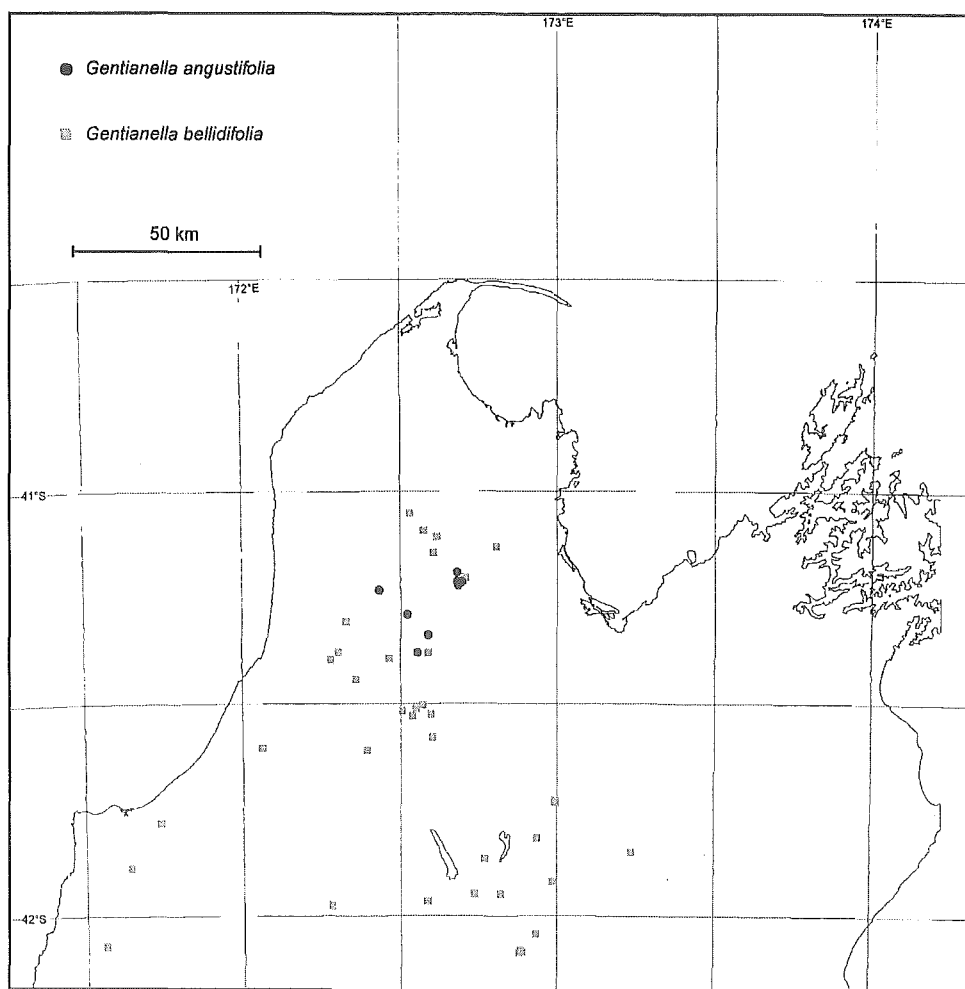


Fig. 48 Distribution of *Gentianella angustifolia*. *G. bellidifolia* is also plotted for comparison.



Fig. 49 *Gentianella angustifolia*, D. Glenny 7365, Granity Pass, CHR 559991. Drawing by Tim Galloway.

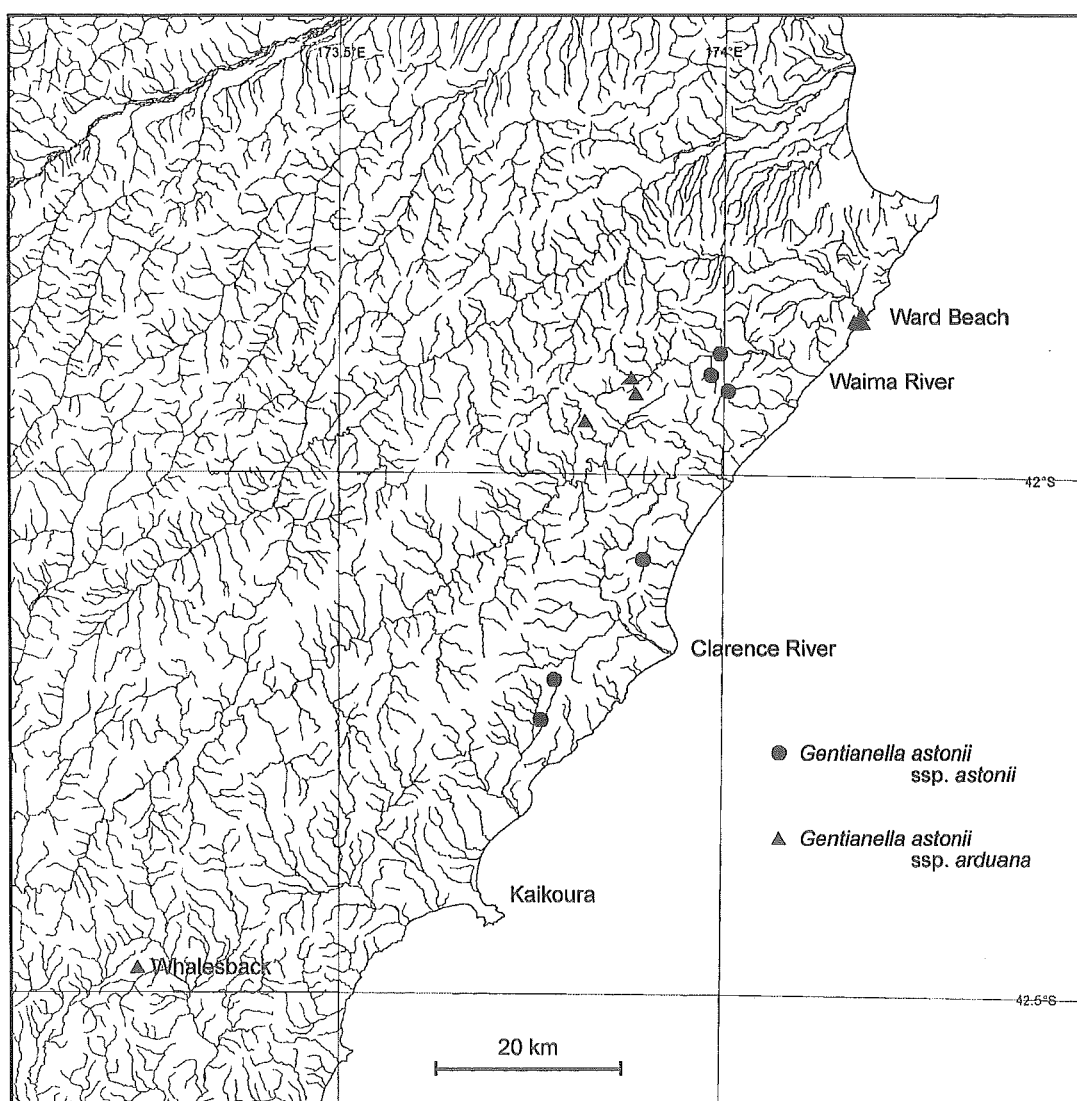


Fig. 50 Distribution of *Gentianella astonii*.

Fig. 51 (right) *Gentianella astonii*
ssp. *arduana*, Weld Cone.



Fig. 52 (below) *Gentianella astonii*
ssp. *astonii* Benmore.
Photo: B. Molloy.



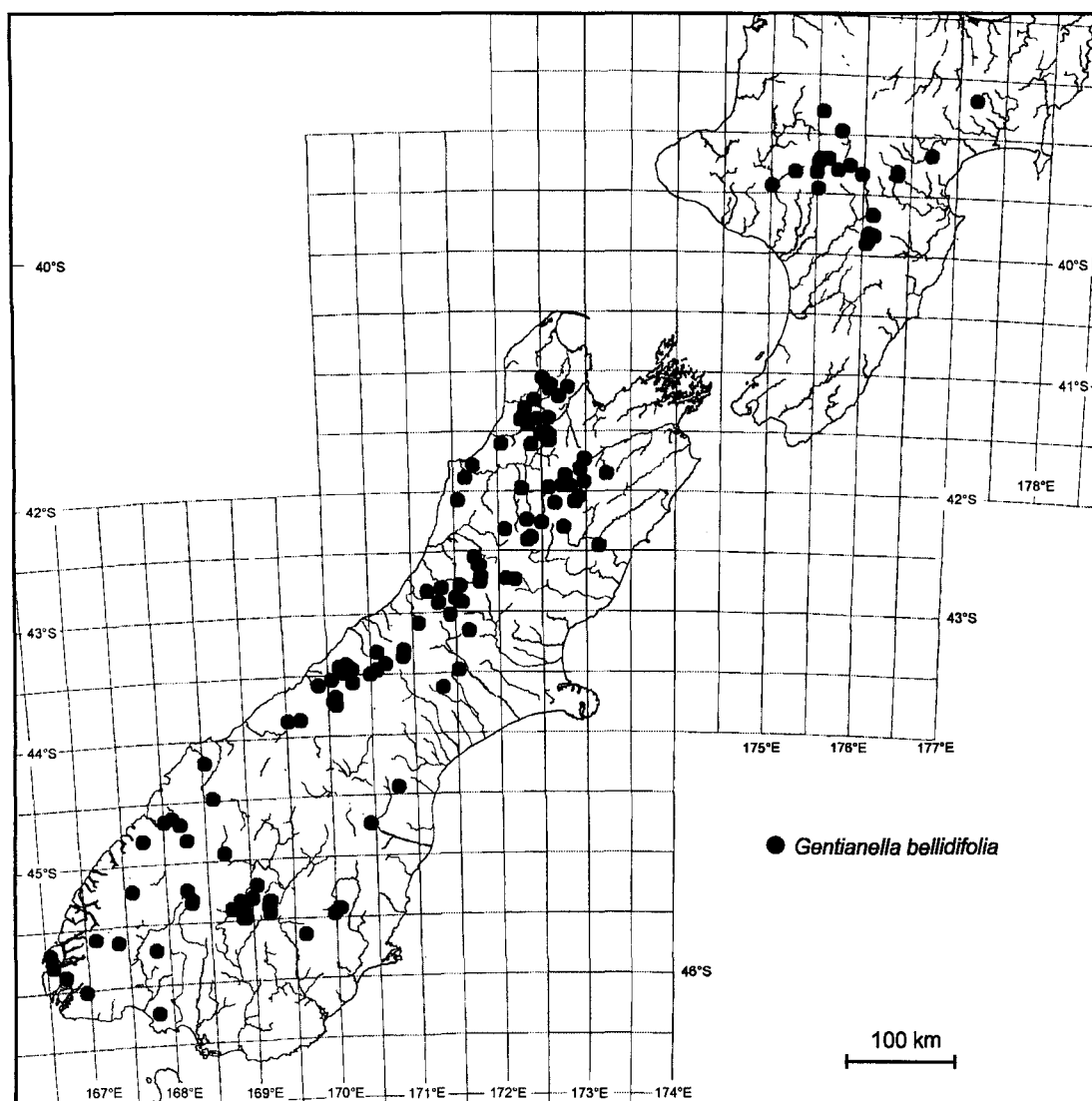


Fig. 53 Distribution of *Gentianella bellidifolia*.



Fig. 54 *Gentianella calcis* ssp. *calcis*, Awahokomo Valley, Kurow.



Fig. 55 *Gentianella calcis* ssp. *manahune*, Manahune Station, Albury.



Fig. 56 *Gentianella chathamica* ssp. *nemorosa*. W. B. Shaw, near L. Waikareiti, CHR 565235. Drawing by Tim Galloway.

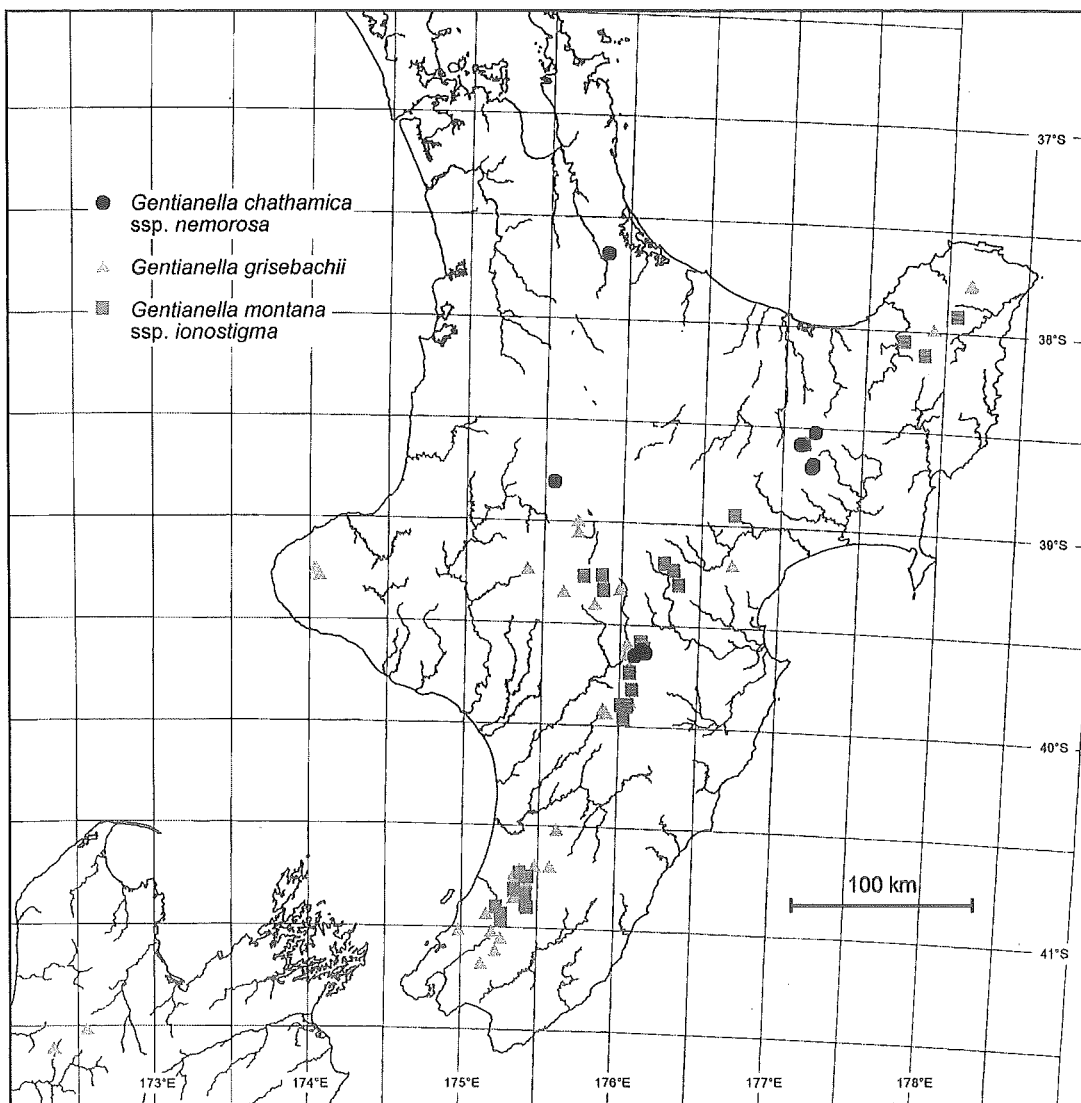


Fig. 57 Distribution of *Gentianella chathamica* ssp. *nemorosa*. *G. grisebachii* and *G. montana* ssp. *nemorosa* are plotted for comparison.

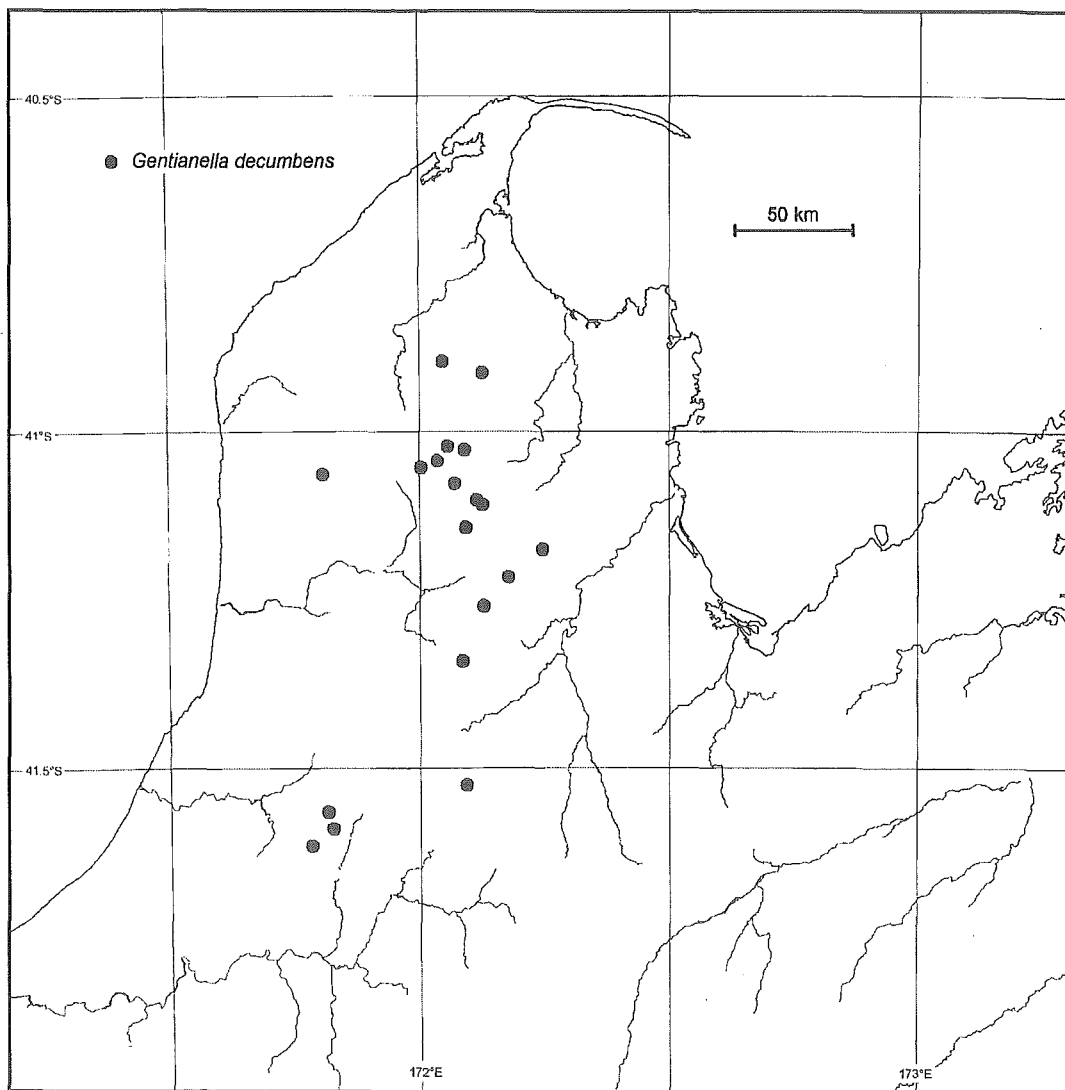


Fig. 58 Distribution of *Gentianella decumbens*.

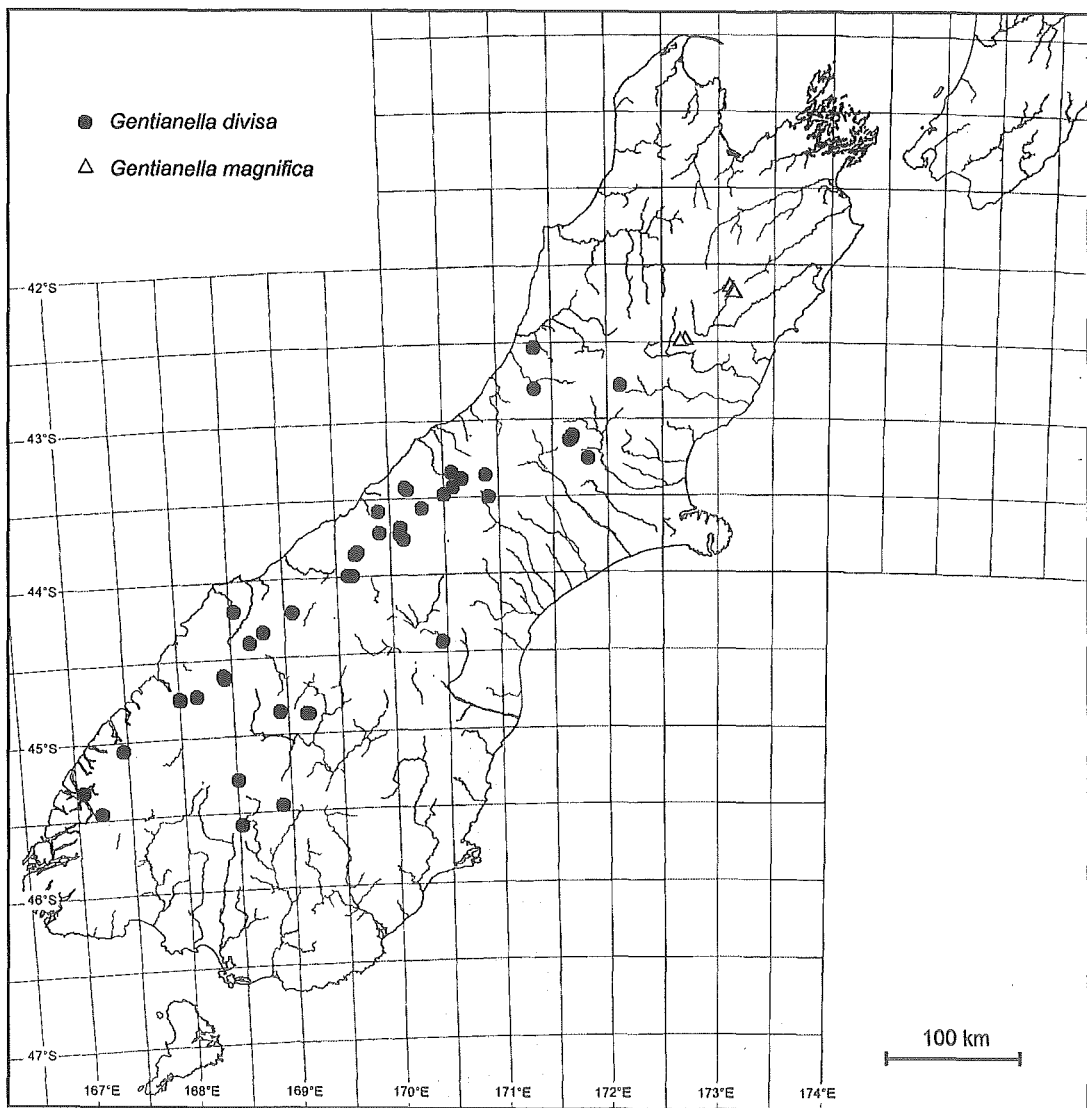


Fig. 59 Distribution of *Gentianella divisa* and *G. magnifica*.

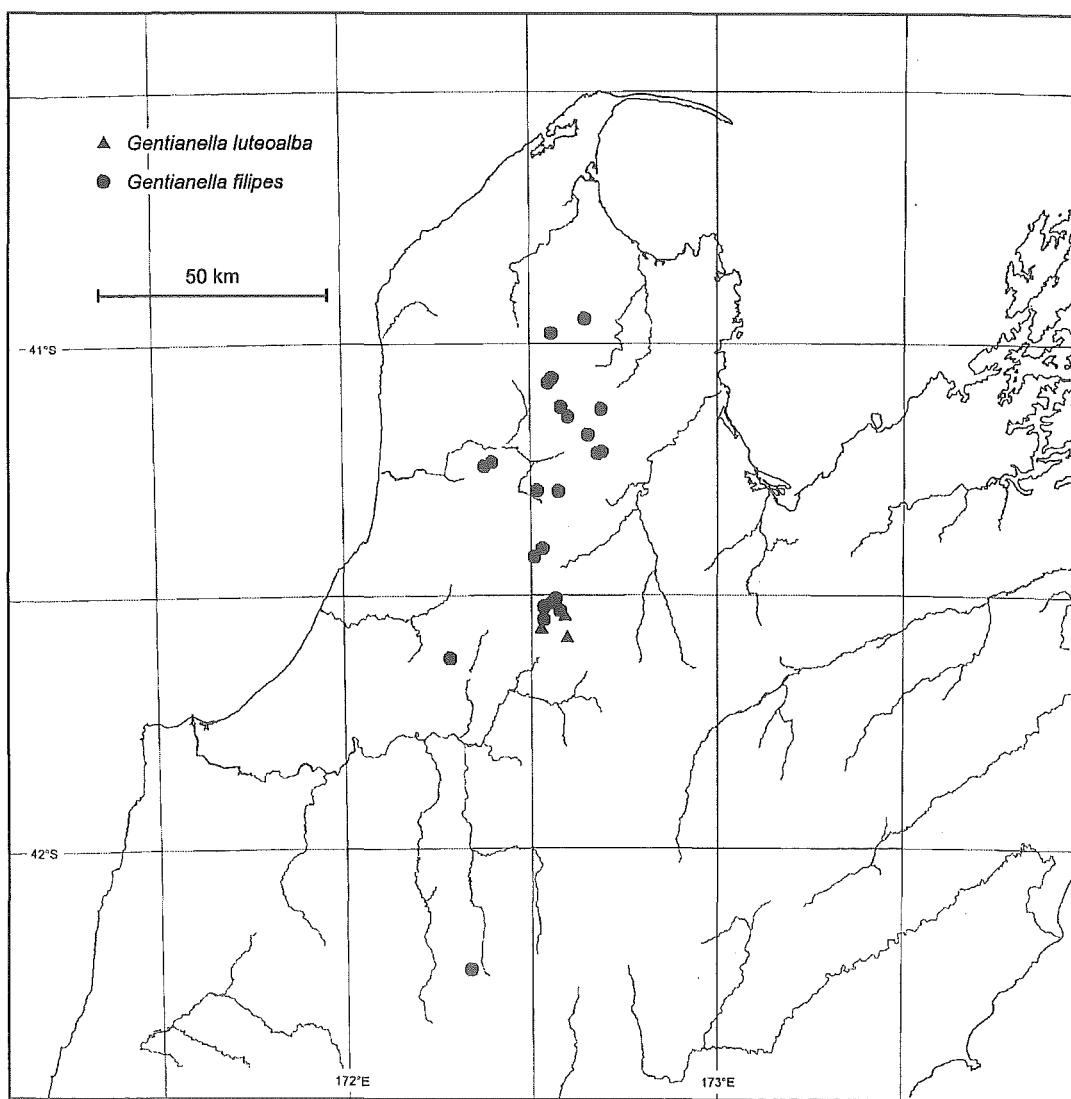


Fig. 60 Distribution of *Gentianella filipes* and *G. luteoalba*.

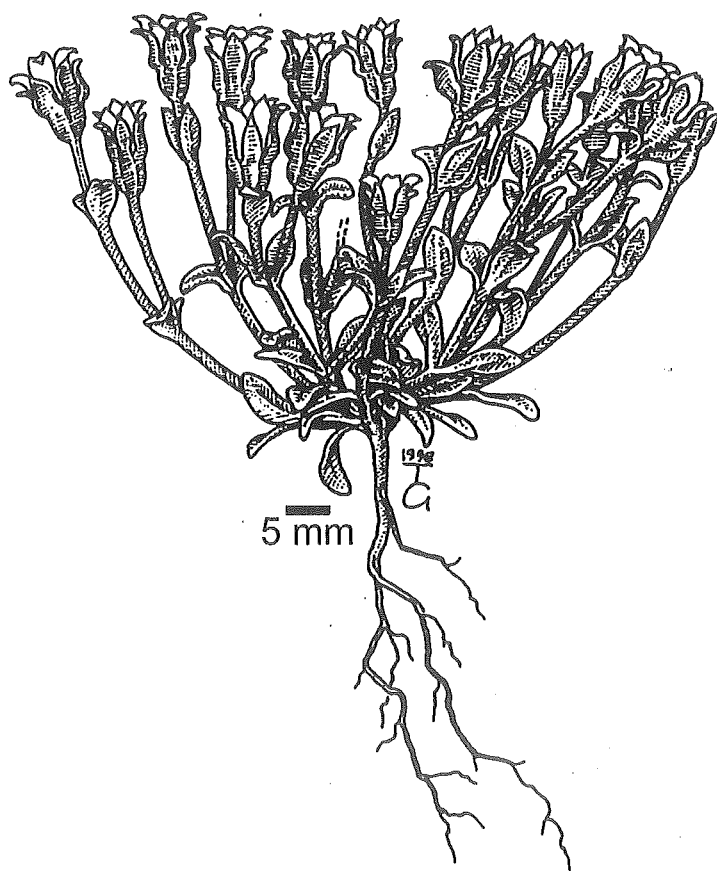


Fig. 61 *Gentianella filipes*. D. Glenny, 7374, Mt Owen, CHR 565002. Drawing by Tim Galloway.



Fig. 62 *Gentianella impressinervia*. K. Ford B/5, Buckland Peaks, CHR 526448. Drawing by Tim Galloway.

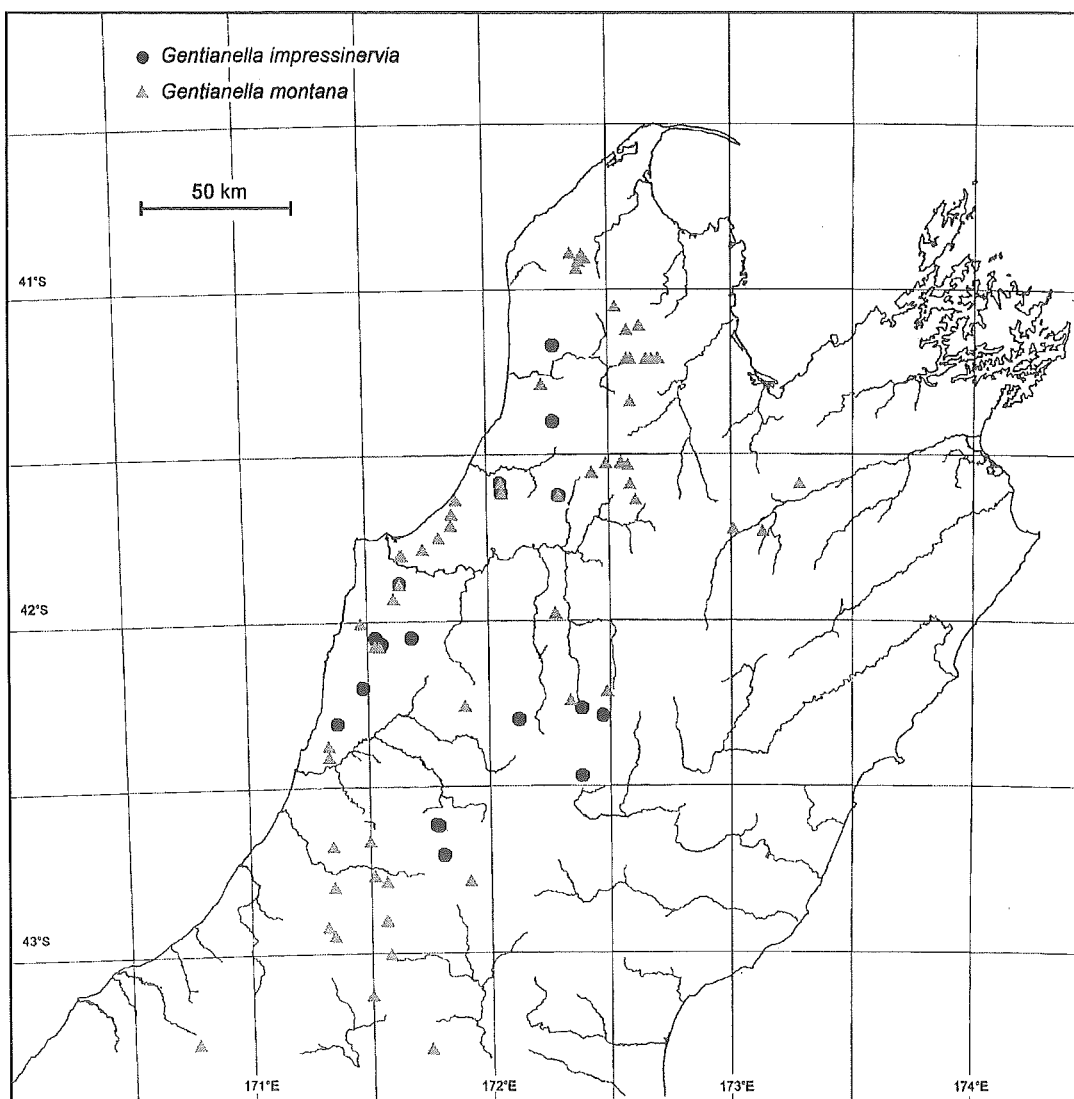


Fig. 63 Distribution of *Gentianella impressinervia*. *G. montana* is also plotted for comparison.

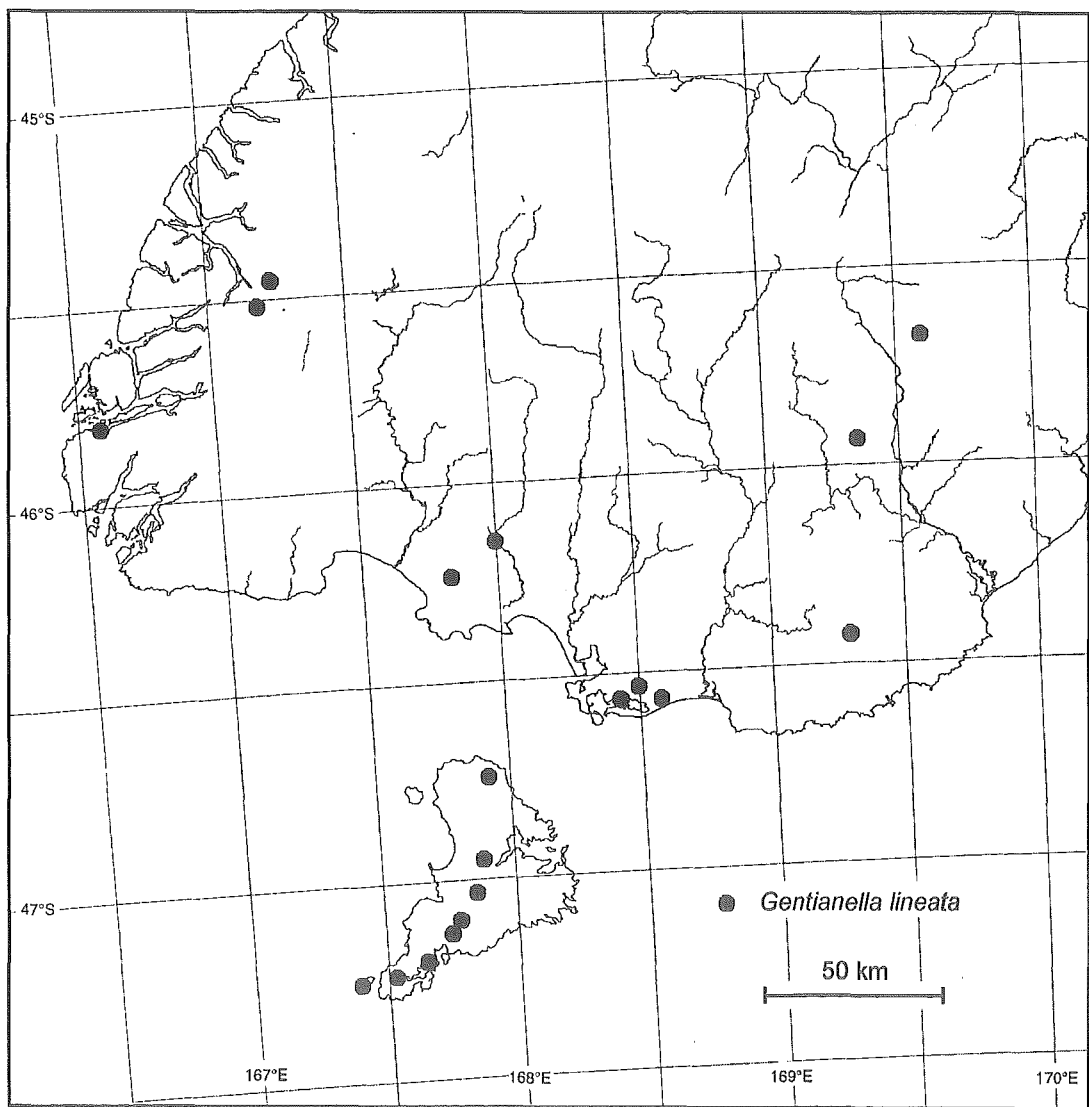


Fig. 64 Distribution of *Gentianella lineata*.

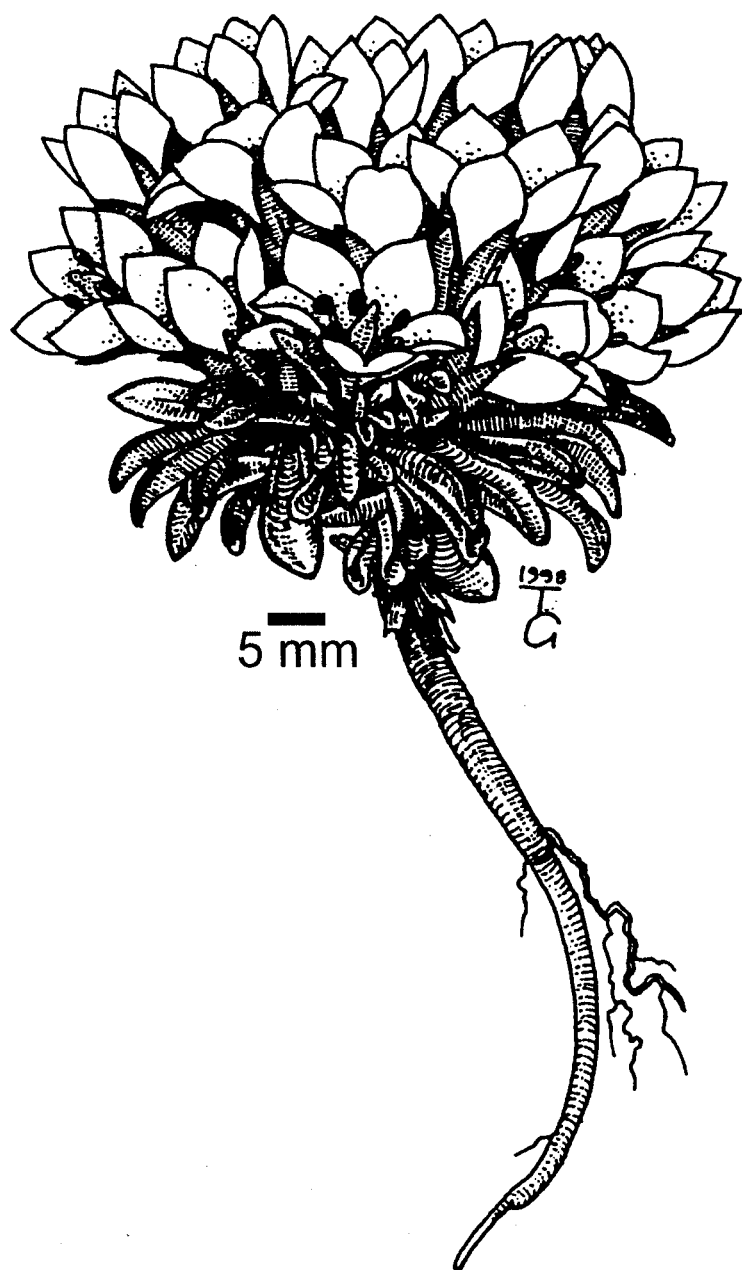


Fig. 65 *Gentianella luteoalba*. D. Glenny 7361, Lookout Range, CHR 559987. Drawing by Tim Galloway.



Fig. 66 *Gentianella magnifica*, Barefell. Photo: J. D. Lovis.

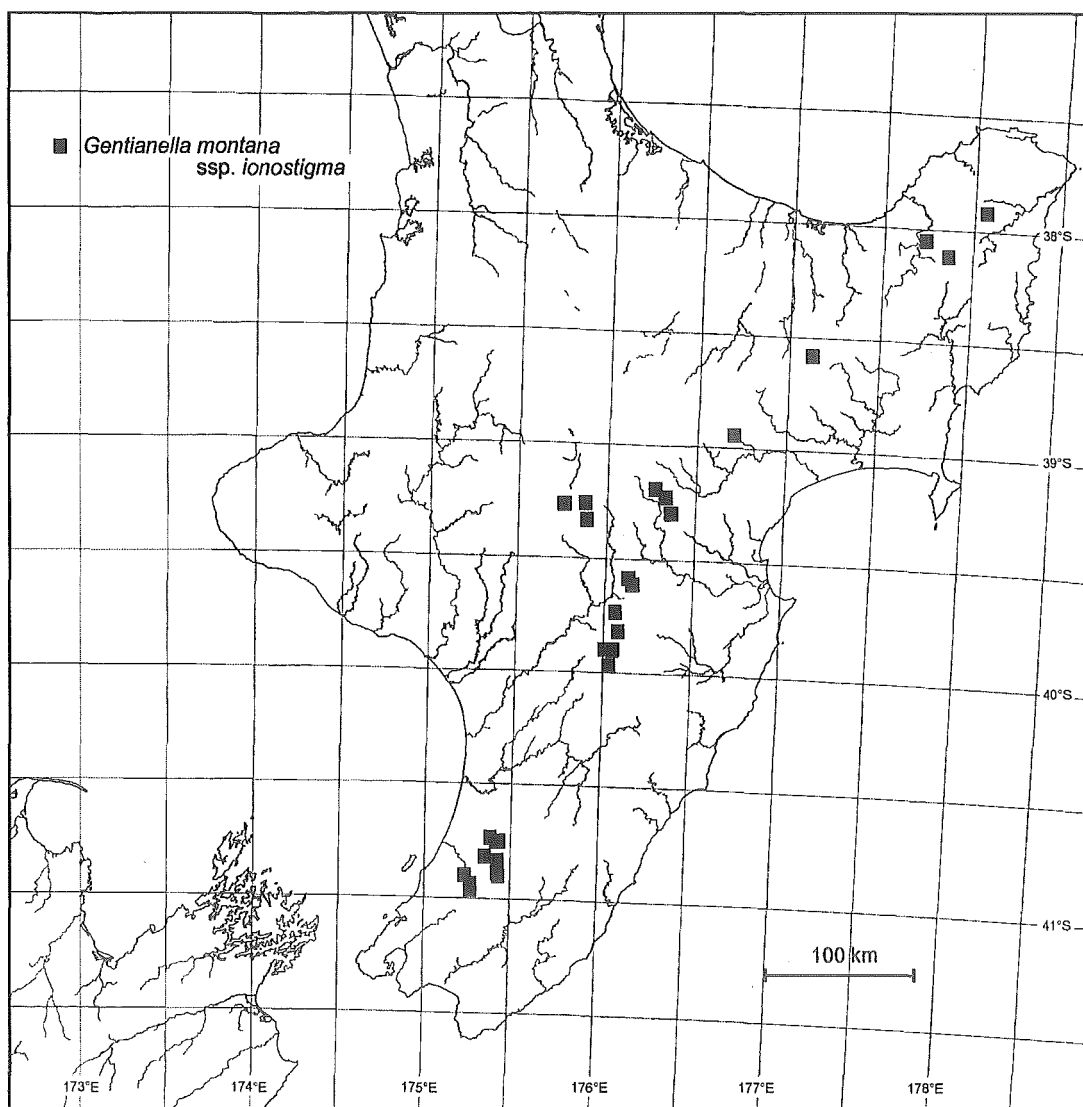


Fig. 67 Distribution of *Gentianella montana* ssp. *ionostigma*.

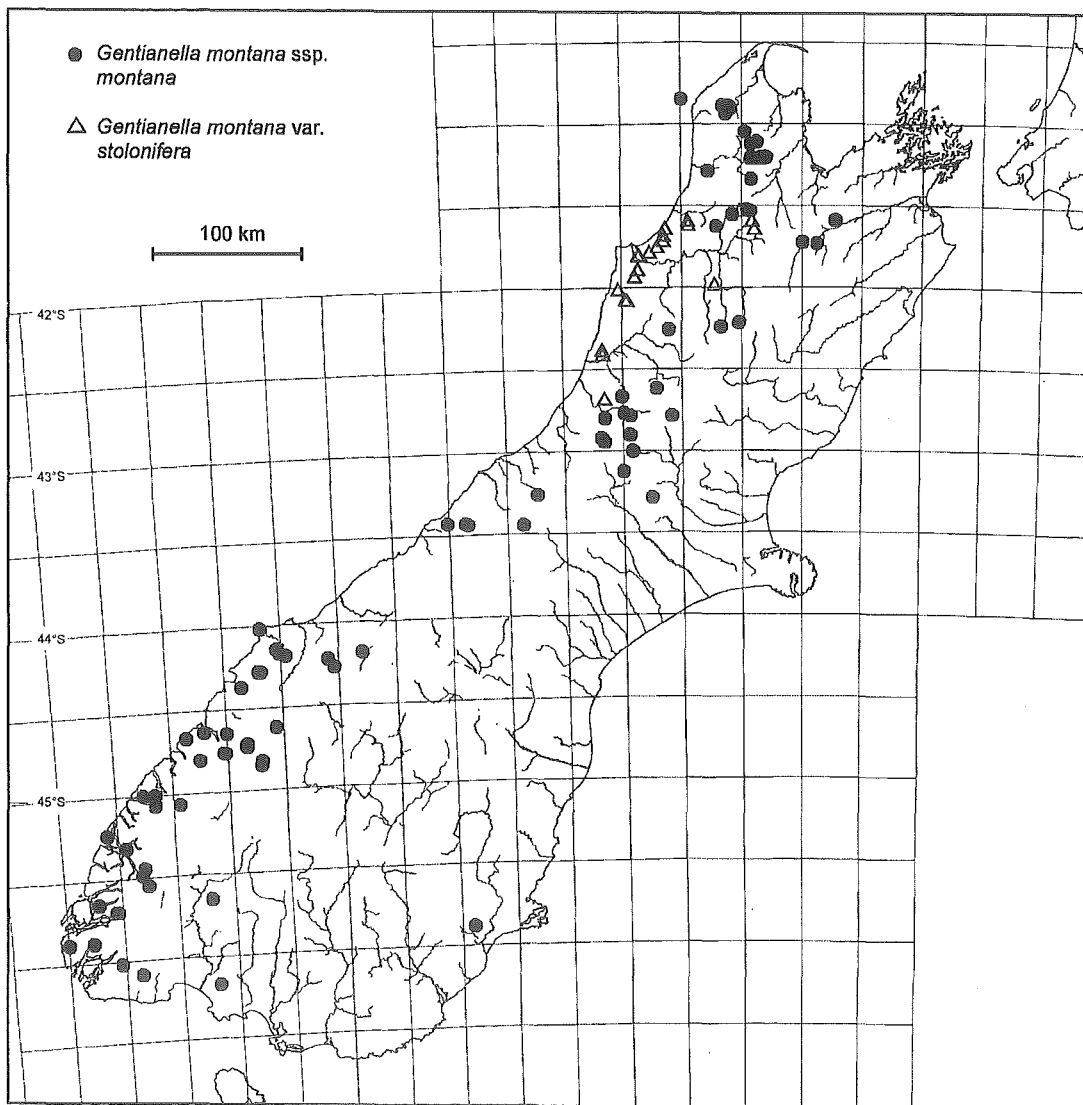


Fig. 68 Distribution of *Gentianella montana* ssp. *montana*, var. *montana* and var. *stolonifera*.

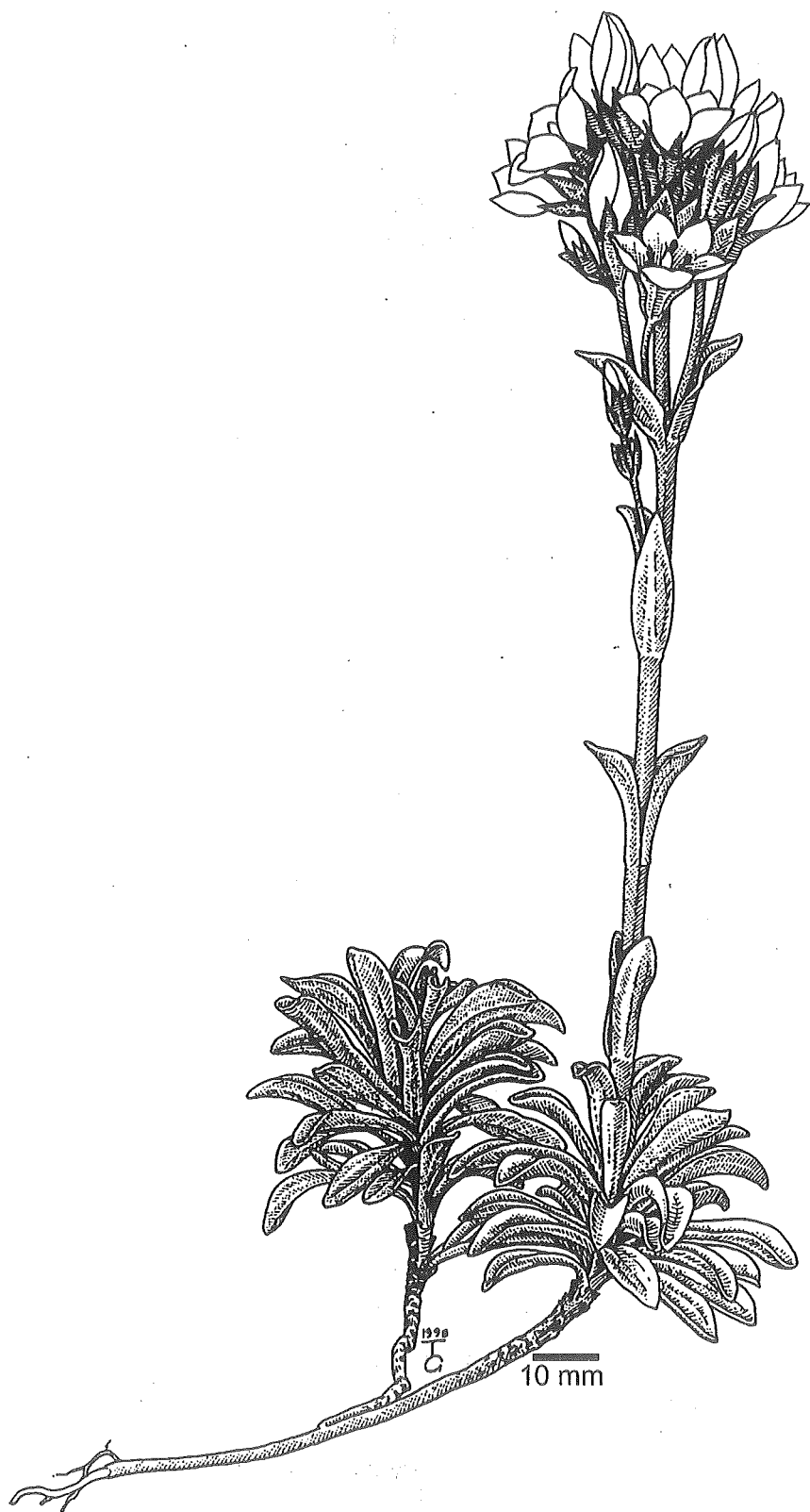


Fig. 69 *Gentianella montana* ssp. *montana* var. *montana*. D. Glenney 6836, Mt Arthur, CHR 559397. Drawing by Tim Galloway.

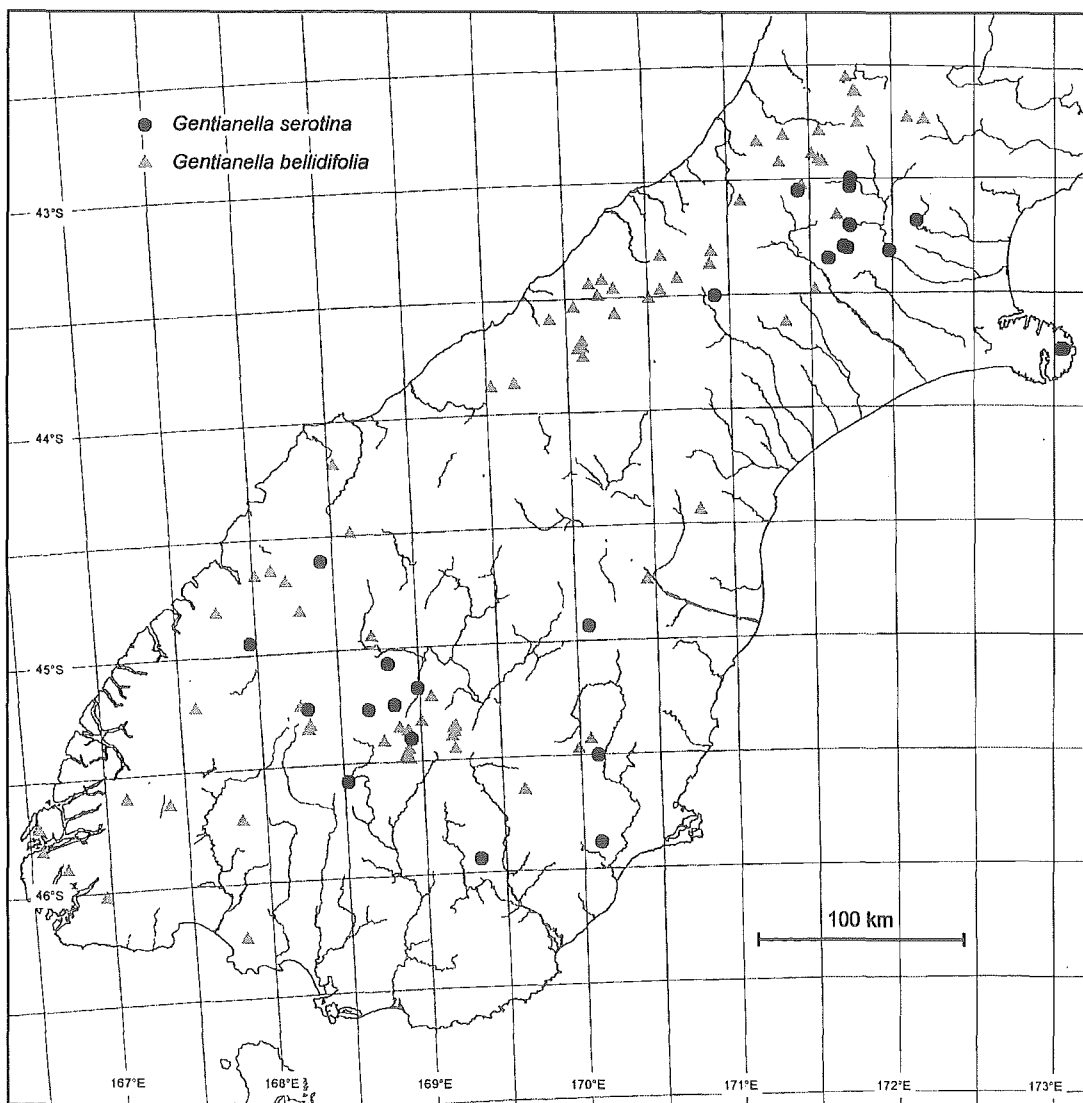


Fig. 70 Distribution of *Gentianella serotina*. *G. bellidifolia* is also plotted for comparison.

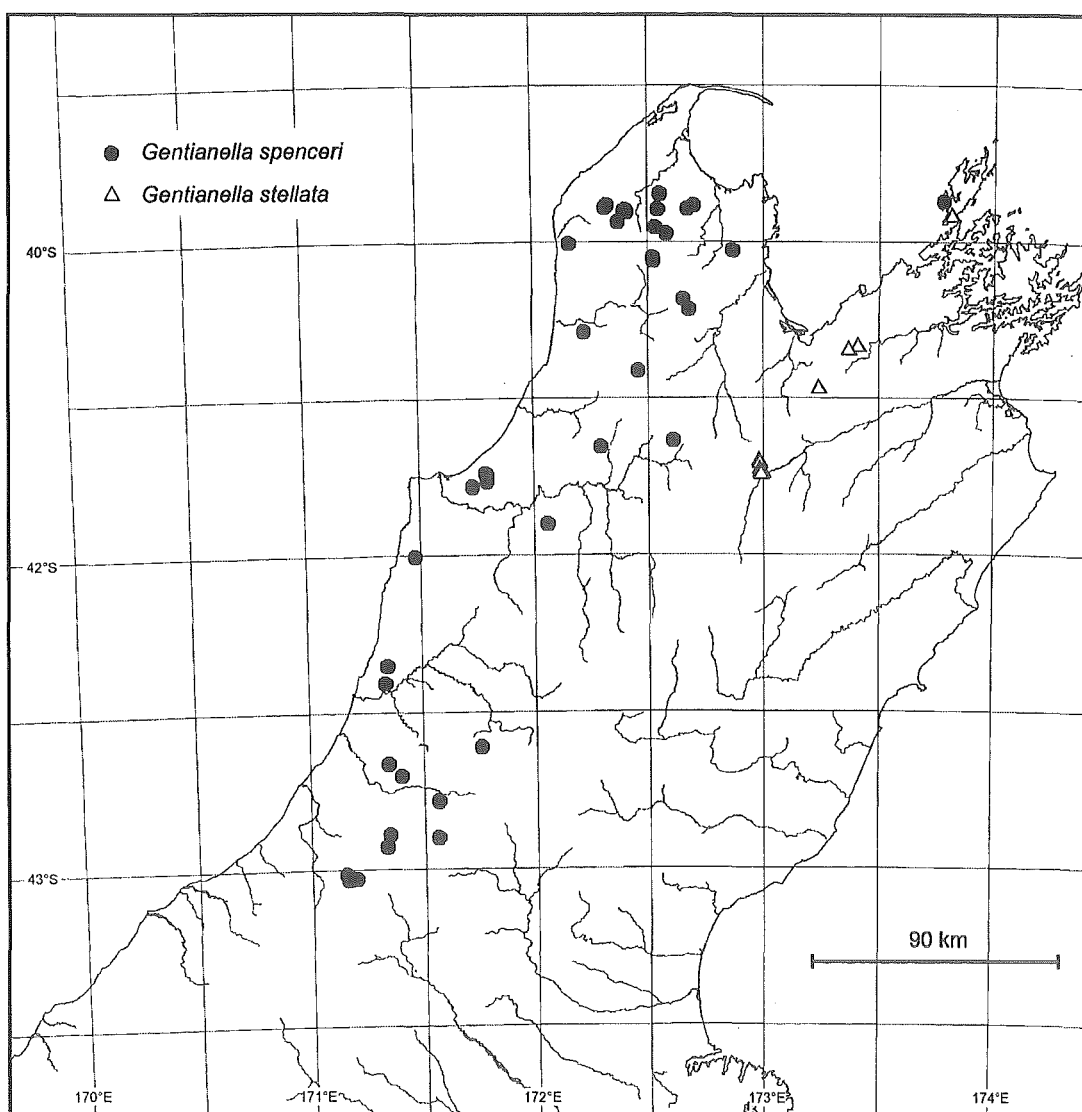


Fig. 71 Distribution of *Gentianella spenceri* and *G. stellata*.

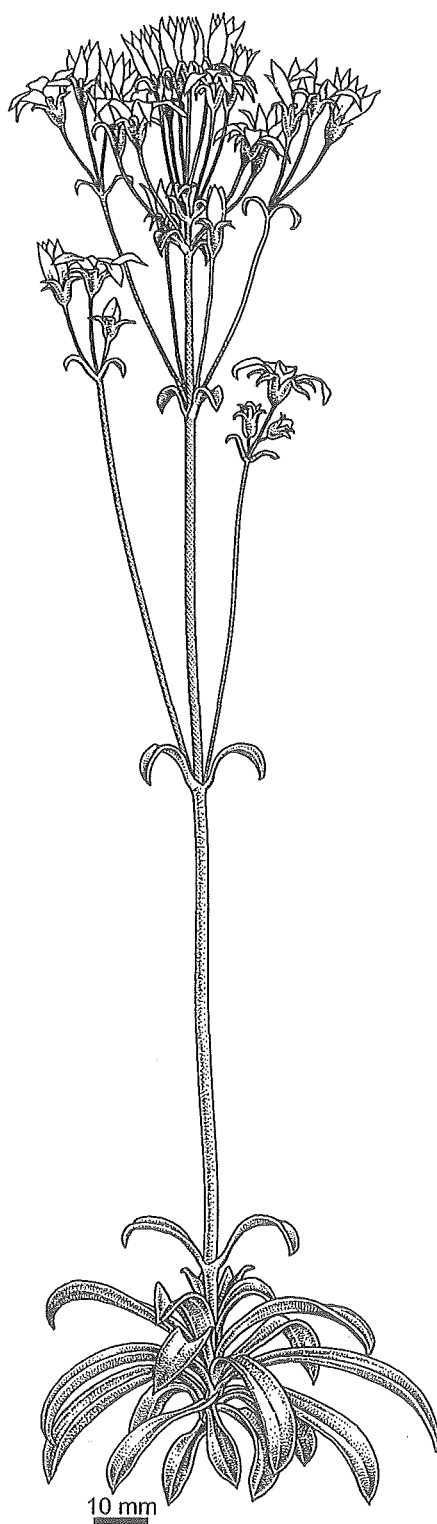


Fig. 72 *Gentianella stellata*. A. P. Druce, D'Urville Island, CHR 387194. Drawing by Tim Galloway.

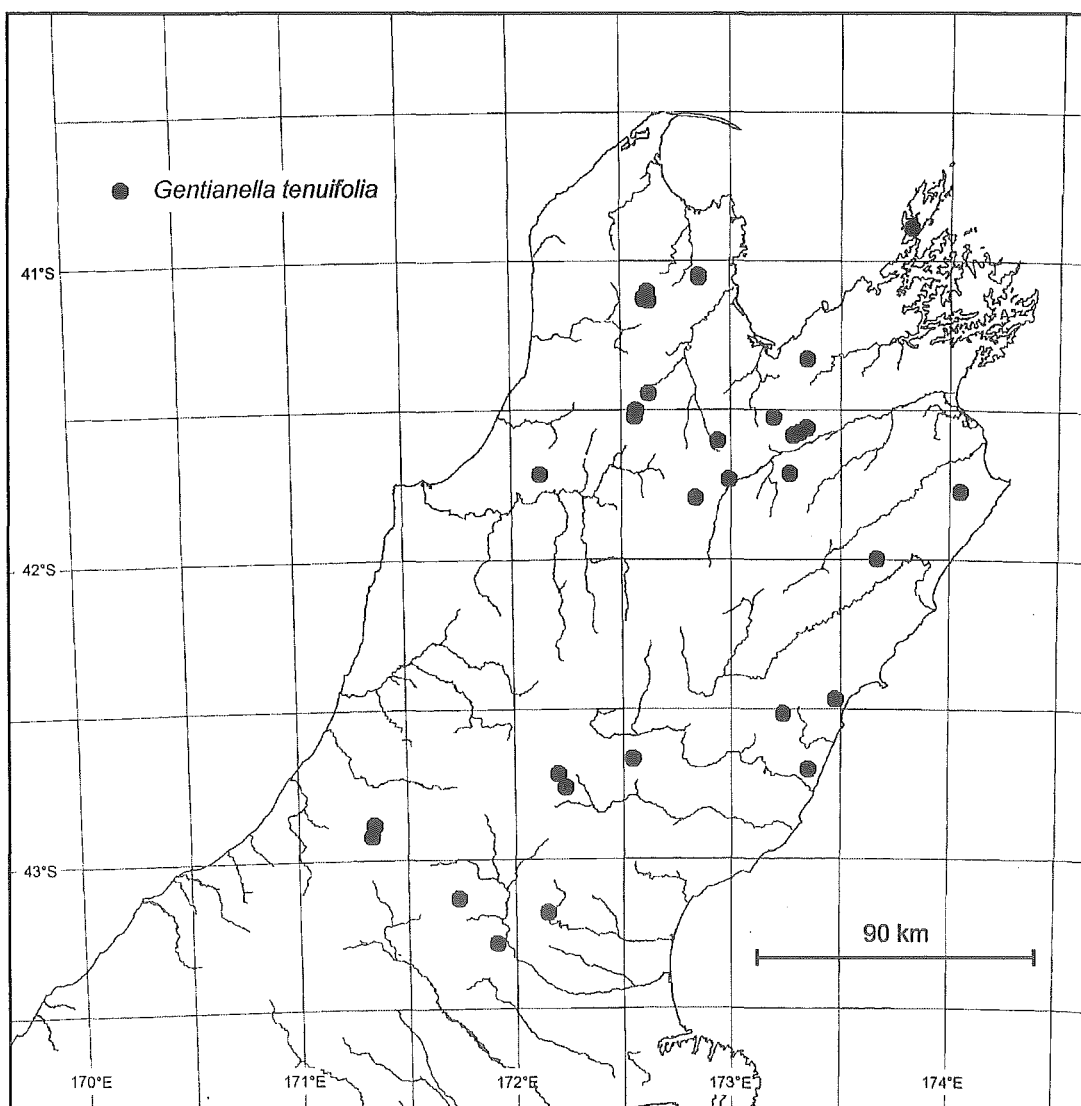


Fig. 73 Distribution of *Gentianella tenuifolia*.



Fig. 74 *Gentianella tenuifolia*. D. Glenny 6776, Red Hills, CHR 530457. Drawing by Tim Galloway.

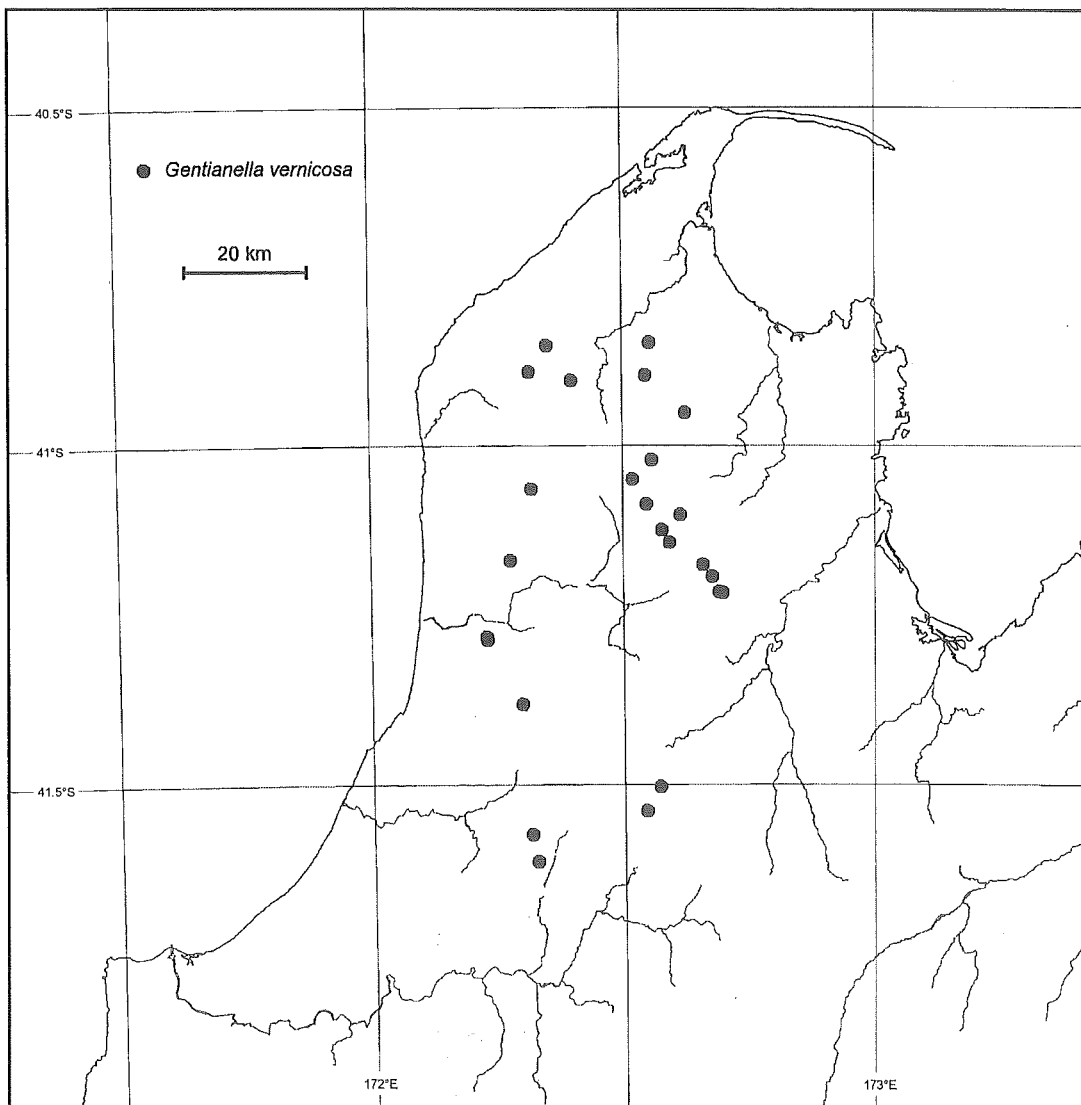


Fig. 75 Distribution of *Gentianella vernicosa*.

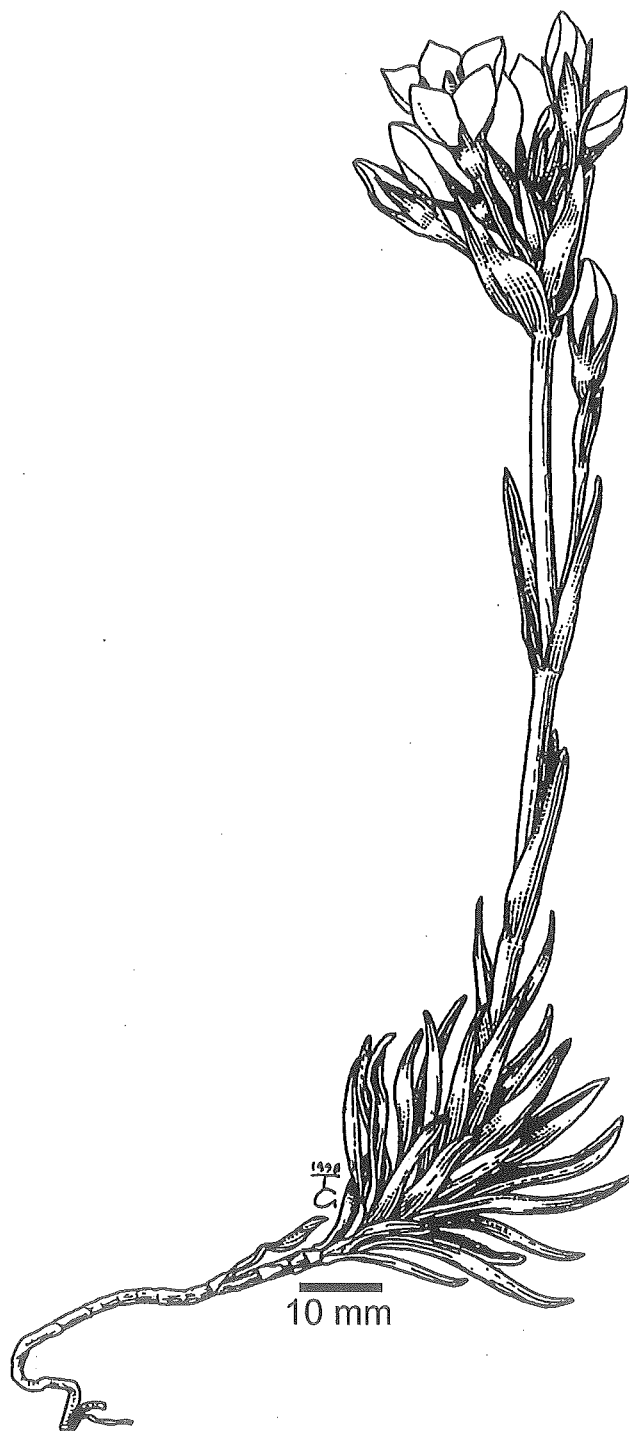


Fig. 76 *Gentianella vernicosa*, D. Glenn 7367a, Sentinel Hill, CHR 559993. Drawing by Tim Galloway.

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APPENDIX I Mophological data set.

G. dianthoides 100002010010112010200?22?0??2?
G. foliosa 110001010010111010110011?1??1?
G. cunninghamii 20000002201000112011001101?010
G. jingerensis 2000010320101011{01}011001101?010
G. ottonis 2100?1010000011000010011?1??1?
G. plantaginea 2000020{13}0010001120{01}1001101?{01}10
G. amabilis 11011203{23}000002{01}200{01}0112011110
G. antarctica 1000020{12}2001110100{12}000{01}0001010
G. angustifolia 210112032100002{01}20010112011011
G. antipoda 1100010{24}1001000100{12}000{01}0001000
G. astonii s. s. 210011030000012020011002012111
G. astonii ssp. *arduana* 210011030010011020211001010111
G. bellidifolia 2{01}01120{13}2000002{01}00{01}10112012110
G. calcis s. s. 21001103001000112000101201?011
G. calcis ssp. *manahune* 21001102001000111011001101?011
G. calcis ssp. *taiko* 21001103001000112000101101?011
G. calcis ssp. *waipara* 21001103{02}01000112001001101?011
G. cerina 210001011000111001{12}10011001000
G. chathamica s. s. 100002021000001010100010011010
G. chathamica ssp. *nemorosa* 100002021000011100110010111010
G. concinna 10000{12}011000101100{12}10011100000
G. corymbifera s. s. 1000021{123}{02}100102{01}100101{01}2010110
G. corymbifera ssp. *gracilis* 000021{123}{02}100101{01}100100{01}1010110
G. decumbens 210112010000002020010011012010
G. divisa 1000021{13}0100102{01}20010111{01}10110{23}
G. filipes 0000000{13}0000000020{02}1001001011{01}5
G. gibbsii 1000020400000010100000110100102
G. grisebachii 1000000{123}200000{12}000{01}{01}001{12}010010{23456}
G. lilliputiana 00000001200000000001001001?0003
G. lineata 21000{01}03{012}0000000000000110111002
G. luteoalba 1000021{13}01000011{12}03100110210105
G. magnifica 1000021101000020200100110100104
G. montana s. s. {12}{01}{01}0021{124}{01}100102{01}2001001201{01}100{2345}
G. montana ssp. *ionostigma* 1{01}00020{23}{12}0001010101100111110?06
G. montana var. *stolonifera* 2110020{123}{24}0001010001100110{01}20?0{45}
G. impressinervia 2110021{24}{014}100102020310112012000{45}
G. patula {12}100020{123}0000101010{01}10011{01}100105
G. saxosa 21000{01}0{23}0001002{01}000100110020102
G. scopulorum 21000201000010101011001100?1104
G. serotina 2101120{123}{012}100101{01}10010012012010{34}
G. spenceri 1000020{12}1000111{01}10110011112010{45}
G. stellata 1000020{234}{01234}100112{01}200100020120105
G. tenuifolia 1000020{12}1100101000110011111010{45}
G. vernicosa 2{01}{01}00203{01}000001020010011002010{45}

Appendix II. List of all specimens seen for the revision.

All specimens at CHR, AK, and OTA were seen in the course of the revision and will all be redetermined or their identity confirmed.

Key to abbreviations in the table headings:

TAXON = name of the taxon, and sometimes an alternative formal or informal name the specimen was considered under for the purpose of analysis.

ACCESSION = herbarium accession number. CHR s.n. indicates a specimen in the Armstrong collection, on loan from CHBG. CHR without a number indicates a voucher was pressed but has not been located and the specimen should be regarded as unvouchered.

DATE = collecting date. xxx = date not recorded from specimen.

P = Cited in the paper prepared from this thesis (D. Glenny 2004, A revision of the genus *Gentianella* in New Zealand. *New Zealand Journal of Botany* 42: 361–530).

A = Fully examined and used for description.

B = Used for data analysis (PCA or t-tests) from a limited set of characters, used to supplement description.

C = Illustrated.

D = Transverse section of leaf examined.

E = DNA extracted and ITS 1 and 2 sequenced.

F = Epidermal cuticle peels examined.

G = Pollen examined with SEM.

H = A type that was seen but not measured for analysis, or a specimen mentioned in the text because of its locality, flower colour, sexuality, etc.

I = Seed size measured with image analyser.

Specimens are ordered by taxon name, Land District, and accession number.

TAXON	LAND DISTRICT	LOCALITY	COLLECTOR	DATE	ACCESSION	P	A	B	C	D	E	F	G	H	I
<i>G. amabilis</i>	OTAGO	Old Woman Range	<i>A. P. Druce</i>	Mar-86	CHR 395767	x		x							
<i>G. amabilis</i>	OTAGO	Garvies	<i>D. Glenny 6383</i>	Feb-96	CHR 509909	x	x	x	x	x					
<i>G. amabilis</i>	OTAGO	Old Man Range	<i>D. Glenny 6406a</i>	Feb-96	CHR 509931B	x		x				x			
<i>G. amabilis</i>	OTAGO	Old Man Range	<i>P. N. Johnson 1375</i>	Feb-97	CHR 511803	x		x	x						
<i>G. amabilis</i>	OTAGO	Cardrona	<i>M. Rixon, P. Thomas, V. Tregidda, M. F. Watson</i>	Feb-98	CHR 523435	x		x							

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<i>G. amabilis</i>	OTAGO	Lammermoor Range	<i>C. Jensen</i>	Mar-97	CHR 526407	x	x	x	x						
<i>G. amabilis</i>	OTAGO	Remarkables	<i>D. Glenney 6862</i>	Feb-97	CHR 559424	x	x	x	x						
<i>G. amabilis</i>	OTAGO	Old Man Range	<i>D. Glenney 6887</i>	Mar-97	CHR 559448	x	x	x	x						
<i>G. androsacea</i>		Ecuador, Cordillera de las Lagunitas	<i>P. M. Jorgensen et al. 832</i>	xxx	MO 4664864	x						x			
<i>G. angustifolia</i>	NELSON	Mt Olive	<i>A. P. Druce</i>	Mar-83	CHR 393808	x	x	x							
<i>G. angustifolia</i>	NELSON	"Turks Cap Range"	<i>A. P. Druce</i>	Feb-89	CHR 395647	x	x	x							
<i>G. angustifolia</i>	NELSON	Hoary Head	<i>A. P. Druce</i>	Feb-86	CHR 395841	x	x	x	x						
<i>G. angustifolia</i>	NELSON	Lookout Range	<i>A. P. Druce 1888</i>	Feb-93	CHR 476152	x	x	x							
<i>G. angustifolia</i>	NELSON	Mt Patriarch	<i>D. Glenney 7748</i>	Feb-99	CHR 525241	x	x	x							
<i>G. angustifolia</i>	NELSON	Mt Arthur	<i>D. Glenney 6834</i>	Feb-97	CHR 530508	x	x	x		x					
<i>G. angustifolia</i>	NELSON	Granity Pass	<i>D. Glenney 7365</i>	Feb-98	CHR 559991	x	x	x	x			x			
<i>G. angustifolia</i>	NELSON	Mt Owen, Sentinel Hill	<i>D. Glenney 7367b</i>	Feb-98	CHR 559994	x	x	x	x						
<i>G. angustifolia</i>	NELSON	Poverty Basin	<i>D. Glenney 7372</i>	Feb-98	CHR 559999	x	x	x							
<i>G. angustifolia</i>	NELSON	Garibaldi Ridge	<i>D. Glenney 7418</i>	Mar-98	CHR 560049	x	x	x	x						
<i>G. angustifolia</i>	NELSON	Mt Arthur	<i>D. Glenney 7440</i>	Mar-98	CHR 560068	x	x	x	x						
<i>G. antarctica</i>		Campbell Is.	<i>D. R. Given 9364</i>	Dec-75	CHR 284793	x							x		
<i>G. antarctica</i>		Campbell Island	<i>C. Meurk</i>	Dec-95	CHR 510016	x					x				
<i>G. antarctica</i>		Campbell Is, Azimuth Hill	<i>E. J. Godley</i>	Jan-69	CHR 549026 spirit collection	x	x								
<i>G. antarctica</i>		Campbell Is, Venus Bog	<i>E. J. Godley</i>	Jan-69	CHR 549028 spirit collection		x		x	x					
<i>G. antarctica</i>		Campbell Island	<i>J. D. Hooker</i>	no date	K (photograph seen)									x	
<i>G. antarctica</i>		Campbell Island	<i>J. D. Hooker</i>	no date	K (photograph seen)									x	
<i>G. antarctica</i>		Campbell Island	<i>T. Kirk</i>	Jan 1890	WELT 4729									x	
<i>G. antarctica</i>		Campbell Island	<i>T. Kirk</i>	Jan 1890	WELT 4730									x	
<i>G. antipoda</i>		Antipodes Is.	<i>R. H. Taylor</i>	Dec-78	CHR 280165		x								
<i>G. antipoda</i>		Antipodes Islands	<i>J. Marris</i>	Nov-95	CHR 510015	x					x				

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<i>G. antipoda</i>		Antipodes Island, "bog 1"	<i>E. J. Godley</i>	Feb-69	CHR 549027 spirit collection.	x	x		x	x		x			
<i>G. antipoda</i>		Antipodes Islands	<i>T. Kirk</i>	Jan 1890	WELT 4731, AK 7332 & 7333									x	
<i>G. antipoda</i>		Antipodes Islands	<i>T. Kirk</i>	Jan 1890	WELT SP55079									x	
<i>G. astonii subsp. arduana</i>	CANTERBURY	Whalesback Ridge	<i>S. Moore</i>	Jan-98	CHR 516238		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Chalk Range	<i>G. Simpson</i>	Feb-33	CHR 109518	x	x	x					x		
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Limestone Quarry hill	<i>W. R. Sykes 556/70</i>	Oct-70	CHR 211891		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Ward Beach	<i>L. B. Moore & Y. Elder</i>	Jul-71	CHR 233840		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	near Flaxbourne River mouth	<i>A. P. Druce</i>	Apr-75	CHR 277526		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Mead Hill	<i>A. P. Druce</i>	Jan-76	CHR 279272		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	"Clarence and the Rivers"	<i>B. C. Aston</i>	Apr-15	CHR 332411	x		x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Weld Cone	<i>B. B. Given & V. Gamble</i>	Apr-79	CHR 356737	x	x	x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Weld Cone	<i>P. J. Garnock-Jones 1996</i>	Oct-90	CHR 470053	x	x	x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Chalk Range	<i>J. S. Thompson and G. Simpson</i>	no date	CHR 515356	x	x	x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Chalk Range	<i>A. Wilton</i>	Feb-98	CHR 516239	x	x			x		x			
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Weld Cone	<i>D. Glenney 7487</i>	Apr-98	CHR 525471	x	x						x		x
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Chalk Range	<i>D. Glenney 7488</i>	Apr-98	CHR 525472	x	x	x	x					x	
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Ward	<i>B. Molloy</i>	Apr-92	CHR 562381	x		x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	hill north of Flaxbourne Creek mouth	<i>G. B. Petterson</i>	Apr-53	CHR 77907	x	x	x							
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Chalk Range	<i>R. Mason & D. McQueen</i>	Dec-53	CHR 84745		x								
<i>G. astonii subsp. arduana</i>	MARLBOROUGH	Flaxbourne River	<i>W. Martin</i>	Apr-23	CHR 93296		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Mt Alexander	<i>D. R. Given 66092</i>	Jan-66	CHR 175137		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Mt Alexander	<i>A. R. Mitchell</i>	Dec-69	CHR 198860		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	NW of Mt Benmore	<i>A. P. Druce</i>	Nov-73	CHR 249199		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Ure River	<i>C. J. Webb</i>	Mar-77	CHR 322733		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Ure Basin	<i>B. C. Aston 882</i>	1915	CHR 332409		x								

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<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Mt Alexander	<i>A. P. Druce</i>	Apr-88	CHR 401292	x	x	x							
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Washdyke Stream	<i>P. A. Williams</i>	May-83	CHR 404729		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Benmore	<i>D. Glenny 6416</i>	Mar-96	CHR 509942	x	x	x	x	x	x				
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Ure River Gorge	<i>G. Simpson</i>	no date	CHR 75730		x								
<i>G. astonii subsp. astonii</i>	MARLBOROUGH	Valley of Ure R.	<i>B. C. Aston</i>	Apr-15	WELT 4726									x	
<i>G. bellidifolia</i>	CANTERBURY	Mt Cook, Sebastopol	<i>D. Glenny 6411</i>	Feb-96	CHR							x			
<i>G. bellidifolia</i>	CANTERBURY	Mt Somers	<i>A. P. Druce</i>	Mar-87	CHR 395857	x		x	x						
<i>G. bellidifolia</i>	CANTERBURY	Arthur's Pass	<i>D. Glenny 6428</i>	Mar-96	CHR 509955	x	x	x	x						
<i>G. bellidifolia</i>	CANTERBURY	Avalanche Peak	<i>D. Glenny 6238</i>	Apr-01	CHR 526391	x		x							
<i>G. bellidifolia</i>	CANTERBURY	Eric Stream	<i>S. Courtney</i>	Mar-96	CHR 526399		x								
<i>G. bellidifolia</i>	CANTERBURY	Punchbowl Creek	<i>D. Glenny 8604</i>	Dec-01	CHR 542509	x			x						
<i>G. bellidifolia</i>	CANTERBURY	Rough Creek	<i>D. Glenny 8489</i>	Apr-01	CHR 526392	x		x							
<i>G. bellidifolia</i>	CANTERBURY	Craigieburn Range, Blackhill	<i>A. Wilton</i>		CHR	x		x							
<i>G. bellidifolia</i>	MARLBOROUGH	Altimarlock	<i>D. Glenny 7781</i>	Mar-99	CHR 525272	x	x	x							
<i>G. bellidifolia</i>	MARLBOROUGH	Altimarlock	<i>K. Hogan 1</i>	Feb-98	CHR 526402	x	x		x			x			
<i>G. bellidifolia</i>	MARLBOROUGH	Altimarlock	<i>G. Jane</i>	Mar-98	CHR 526406	x	x	x							
<i>G. bellidifolia</i>	MARLBOROUGH	No Mans Creek	<i>D. Glenny 6898</i>	Mar-97	CHR 530571	x		x	x						
<i>G. bellidifolia</i>	MARLBOROUGH	No Mans Creek	<i>D. Glenny 6899</i>	Mar-97	CHR 530572A-J	x	x	x	x					x	
<i>G. bellidifolia</i>	MARLBOROUGH	Turks Head Saddle NLNP, saddle between Mole Stream and Bruce Creek	<i>M. J. A. Simpson 879 & R. V. Mirams</i>	Feb-53	CHR 80810									x	
<i>G. bellidifolia</i>	NELSON	Cobb Valley	<i>M. J. A. Simpson 4168</i>	Feb-64	CHR 148807									x	
<i>G. bellidifolia</i>	NELSON	Cobb Valley	<i>A. P. Druce</i>	Mar-70	CHR 252213	x			x						
<i>G. bellidifolia</i>	NELSON	Red Hills	<i>A. P. Druce</i>	May-74	CHR 273146	x		x						x	
<i>G. bellidifolia</i>	NELSON	Marino Mtns, Reverse Basin	<i>C. J. Webb 7666</i>	Jan-76	CHR 283739									x	
<i>G. bellidifolia</i>	NELSON	Mt Peel	<i>B. Macmillan 89/46</i>	Feb-89	CHR 327058									x	
<i>G. bellidifolia</i>	NELSON	Faerie Queen	<i>W. D. Burke 200</i>	Feb-85	CHR 420768	x			x						

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<i>G. bellidifolia</i>	NELSON	Marino Mtns, Sanctuary Basin	<i>D. Glenny 6297</i>	Jan-96	CHR 509816.	x					x				
<i>G. bellidifolia</i>	NELSON	Right Branch Motueka River	<i>D. Glenny 6432</i>	Mar-96	CHR 509959	x	x		x						
<i>G. bellidifolia</i>	NELSON	Buckland Peaks	<i>D. Glenny 6450</i>	Mar-96	CHR 509977		x		x						
<i>G. bellidifolia</i>	NELSON	Buckland Peaks	<i>D. Glenny 6450</i>	Mar-96	CHR 509977	x			x						
<i>G. bellidifolia</i>	NELSON	Lewis Pass	<i>M. Newfield</i>	Feb-98	CHR 517483	x		x	x						
<i>G. bellidifolia</i>	NELSON	Rahu Stream	<i>P. Wardle</i>	1996	CHR 565237	x		x	x						
<i>G. bellidifolia</i>	NELSON	Red Hills	<i>D. Glenny 6438</i>	Mar-96	CHR 590960	x		x			x				
<i>G. bellidifolia</i>	NELSON	St Arnaud Range	<i>G. Jane</i>	xxx	unvouchered				x						
<i>G. bellidifolia</i>	OTAGO	Hyde Rock	<i>D. R. Given 14216</i>	Feb-86	CHR 420574	x			x						
<i>G. bellidifolia</i>	OTAGO	Old Man Range	<i>D. Glenny 6406</i>	Feb-96	CHR 509931	x						x			
<i>G. bellidifolia</i>	OTAGO	Waikaia Bush Road	<i>P. N. Johnson 1370</i>	Feb-97	CHR 511798				x						
<i>G. bellidifolia</i>	OTAGO	Old Man Range	<i>P. N. Johnson 1373</i>	Feb-97	CHR 511801	x	x		x			x			
<i>G. bellidifolia</i>	OTAGO	Rock and Pillar Range	<i>P. D. Scott</i>	no date	OTA 036452	x			x						
<i>G. bellidifolia</i>	SOUTHLAND	Eyre Mtns, Helen Peaks	<i>B. Rance</i>	Mar-98	CHR 516251									x	
<i>G. bellidifolia</i>	SOUTHLAND	Eyre Mountains	<i>R. McKenzie</i>	Apr-98	CHR 518954	x		x	x						
<i>G. bellidifolia</i>	SOUTHLAND	Livingstone Mountains	<i>P. N. Johnson 1398</i>	Jan-98	CHR 526298	x	x		x						
<i>G. bellidifolia</i>	SOUTHLAND	Takitimu Mountains	<i>B. Rance</i>	Mar-97	CHR 526414	x	x	x	x						
<i>G. bellidifolia</i>	SOUTHLAND	Fiordland, End Peak	<i>J. Crosby Smith</i>	no date	WELT 4713									x	
<i>G. bellidifolia</i>	WELLINGTON	Kaweka Range	<i>M. J. Bayly 880</i>	Jan-98	CHR 516237	x	x		x						
<i>G. bellidifolia</i>	WELLINGTON	Kaimanawa Mountains	<i>C. Ecroyd</i>	Apr-99	CHR 526294	x	x	x							
<i>G. bellidifolia</i>	WELLINGTON	Tongariro	<i>I. Breitwieser 2081</i>	Jan-98	CHR 526297	x	x	x	x						
<i>G. bellidifolia</i>	WELLINGTON	Ruahine Range	<i>S. Wagstaff 97-130</i>	Apr 1997	CHR 526418	x	x	x	x						
<i>G. bellidifolia</i>	WELLINGTON	Tongariro	<i>J. C. Bidwill</i>	no date	K (photograph seen)									x	
<i>G. bellidifolia</i>	WELLINGTON	Ruapehu	<i>A. Wilton 99105B</i>	Feb-99	CHR 518977	x	x	x	x						
<i>G. bellidifolia</i>	WESTLAND	Camp Creek	<i>K. Ford 1/CK</i>	Apr-96	CHR 526293		x								
<i>G. bellidifolia</i>	WESTLAND	Harman Pass	<i>D. Glenny 6931</i>	Apr-97	CHR 530600	x	x	x	x						

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<i>G. bellidifolia</i>	WESTLAND	Westland, Trent Saddle	<i>D. Glenny 6925</i>	Mar-97	CHR 559482	x	x	x							
<i>G. bellidifolia</i>	WESTLAND	Moeraki River, Lake Sweeney	<i>D. Glenny 7383</i>	Feb-98	CHR 560013	x		x	x						
<i>G. bellidifolia</i>	WESTLAND	Otira, Kelly's Hill	<i>D. Petrie</i>	Jan 1893	WELT 47177		x							x	
<i>G. bellidifolia</i>	WESTLAND	Mt Barron	<i>A. Wood</i>		CHR	x		x							
<i>G. bellidifolia</i>	WESTLAND	Mt Barron	<i>A. Wood</i>		CHR	x		x							
<i>G. bellidifolia</i> "Red Hills Pear"	MARLBOROUGH	Red Hills	<i>D. Glenny 7438</i>	Mar-98	CHR					x					
<i>G. bellidifolia</i> x <i>G. lilliputiana</i>	OTAGO	Dunstan Mountains	<i>D. Bruce</i> <i>J. C. Solomon & M. Moraes</i>	Jan-85	CHR 461350									x	
<i>G. boliviana</i>		Bolivia, Murillo Prov., Milluni	<i>13462</i> <i>P. J. de Lange 2796 & G. M. Crowcroft</i>	xxx	MO 3305338.	x						x			
<i>G. calcis subsp. calcis</i>	OTAGO	Awahokomo		Dec-94	AK 490856		x								
<i>G. calcis subsp. calcis</i>	OTAGO	Awahokomo	<i>B. Molloy</i>	Apr-95	CHR 529113	x	x	x						x	
<i>G. calcis subsp. calcis</i>	OTAGO	Awahokomo	<i>D. Glenny 8234</i>	May-00	CHR 560262	x	x	x	x						
<i>G. calcis subsp. manahune</i>	CANTERBURY	Manahune Station	<i>B. Molloy</i>	May-92	CHR 542276	x	x	x							
<i>G. calcis subsp. manahune</i>	CANTERBURY	Manahune Station	<i>D. Glenny 8232 & B. Molloy</i>	May-00	CHR 560259	x	x	x	x						
<i>G. calcis subsp. taiko</i>	CANTERBURY	Limestone Valley, Taiko junction of Limestone Valley Road and McLeods Road	<i>A. E. Woodhouse</i>	Apr-69	CHR 191742		x								
<i>G. calcis subsp. taiko</i>	CANTERBURY	Limestone Valley Road	<i>B. H. Macmillan 73/481</i>	Apr-73	CHR 256518		x								
<i>G. calcis subsp. taiko</i>	CANTERBURY	Limestone Valley Road	<i>B. Molloy</i>	Apr-92	CHR 529111	x	x	x							
<i>G. calcis subsp. taiko</i>	CANTERBURY	Limestone Valley Road	<i>D. Glenny 8233</i>	May-00	CHR 560260	x	x	x	x						
<i>G. calcis subsp. waipara</i>	CANTERBURY	Mt Donald	<i>A. J. Healy</i>	May-41	CHR 33424	x	x	x							
<i>G. calcis subsp. waipara</i>	CANTERBURY	Weka Pass	<i>A. P. Druce</i>	Mar-87	CHR 394403	x	x	x							
<i>G. calcis subsp. waipara</i>	CANTERBURY	South Dean	<i>A. W. Robertson</i>	Jan-86	CHR 419784		x								
<i>G. calcis subsp. waipara</i>	CANTERBURY	Mt Brown	<i>B. Molloy</i>	Apr-92	CHR 529112	x	x	x							
<i>G. calcis subsp. waipara</i>	CANTERBURY	Mt Brown	<i>D. Glenny 7456</i>	Mar-98	CHR 560083	x	x	x	x						
<i>G. calcis subsp. waipara</i>	OTAGO	Duntroon	<i>J. Barkla</i>	May-04	CHR 569771	x	x	x							
<i>G. cerina</i>		Auckland Island, Mt Eden	<i>E. J. Godley</i>	Dec-62	CHR 134051									x	
<i>G. cerina</i>		Auckland Island	<i>W. H. Dawbin</i>	Feb-43	CHR 368904									x	

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<i>G. cerina</i>		Auckland Is., Enderby I.	<i>C. Meurk</i>	Dec-85	CHR 510018	x	x		x	x	x				
<i>G. cerina</i>		Auckland Islands	<i>J. D. Hooker</i>	1845	K (photograph seen)									x	
<i>G. cerina</i>		Auckland Is.	<i>D. J. Campbell</i>	xxx	WELT 11170 (not seen)								x		
<i>G. cerina</i>		Adams Island, Carnley Harbour	<i>T. Kirk</i>	Jan 1890	WELT 4728, K (photograph seen)									x	
<i>G. chathamica subsp. chathamica</i>		Chatham Islands	<i>F. A. D. Cox</i>	no date	AK 7181									x	
<i>G. chathamica subsp. chathamica</i>		Chatham Island, near Awatotara River	<i>W. Sykes 497/93</i>	Dec-93	CHR 496871	x	x	x							
<i>G. chathamica subsp. chathamica</i>		Chatham Island	<i>P. J. de Lange CH21</i>	Feb-96	CHR 510011	x	x	x	x	x	x				
<i>G. chathamica subsp. chathamica</i>		Chatham Island, Tuku-a-tamatea River	<i>D. Glenny 7260</i>	Dec-97	CHR 526291	x	x	x					x		
<i>G. chathamica subsp. chathamica</i>		Chatham Is, Waimahana Creek	<i>D. Glenny 7152</i>	Dec-97	CHR 559759	x	x	x	x			x			
<i>G. chathamica subsp. chathamica</i>		Chatham Islands	<i>F. A. D. Cox</i>	no date	WELT 47795									x	
<i>G. chathamica subsp. nemorosa</i>	GISBORNE	NE of Lake Waikareiti, Sopps Clearing	<i>W. B. Shaw</i>	Feb-99	CHR 565235	x	x	x	x						
<i>G. chathamica subsp. nemorosa</i>	WELLINGTON	Kaimanawa Mountains	<i>A. P. Druce</i>	Feb-57	CHR 112770	x			x						
<i>G. chathamica subsp. nemorosa</i>	WELLINGTON	Kaimanawa Mountains	<i>A. P. Druce</i>	Feb-85	CHR 402272	x	x	x							
<i>G. chathamica subsp. nemorosa</i>	WELLINGTON	Whakapapa	<i>S. Deverill</i>	Apr-00	CHR 541819	x	x	x							
<i>G. chathamica subsp. nemorosa</i>	WELLINGTON	Hauhangatahi	<i>L. B. Moore</i>	Feb-57	CHR 87812	x	x	x							
<i>G. concinna</i>		Auckland Island	<i>W. R. Sykes</i>	Feb-87	CHR 437301	x							x		
<i>G. concinna</i>		Auckland Island, Tagua Bay Isthmus	<i>C. Meurk</i>	Dec-95	CHR 526412	x	x		x	x		x			
<i>G. concinna</i>		Auckland Islands	<i>J. D. Hooker</i>	1845	K (photograph seen)									x	
<i>G. corymbifera</i>	NELSON	Culliford Hill	<i>D. Glenny 7719</i>	Feb-99	CHR 525492									x	
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Upper Clarence Valley, nr L. Tennyson	<i>D. Glenny 6281</i>	Jan-96	CHR 509799	x	x	x					x		
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Mt Cook	<i>D. Glenny 6408</i>	Feb-96	CHR 509935	x	x				x				
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Mt Cook	<i>D. Glenny 6412</i>	Feb-96	CHR 509938		x								
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Ohau, Freehold Creek	<i>N. Simpson</i>	Jan-97	CHR 526299	x	x	x	x						
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Rough Creek	<i>D. Glenny 8490</i>	Apr-01	CHR 526393	x		x							
<i>G. corymbifera subsp. corymbifera</i>	CANTERBURY	Mt Cook, Kea Flat	<i>D. Banks</i>	no date	CHR 526453	x			x						

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<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Broken River	<i>D. Glenny</i> 6903	Mar-97	CHR 559461	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Ohau Range	<i>D. Glenny</i> 7347	Feb-98	CHR 560149		x								
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Ohau Range	<i>D. Glenny</i> 7351	Feb-98	CHR 560153		x								
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Maitland Stream	<i>B. Brown</i>	xxx	unvouchered		x								
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Canterbury Plains	<i>J. B. Armstrong</i>	no date	WELT 4716										
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Amuri, St James Station	<i>T. Kirk</i>	no date	WELT 4719									x	
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	above Jollies Pass	<i>Heinrich von Haast</i>	no date	WELT 47817									x	
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	CANTERBURY	Mt Oxford	<i>G. Spearpoint</i>	Mar-99	CHR	x		x							
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	MARLBOROUGH	Altimarlock	<i>D. Glenny</i> 7784	Mar-99	CHR 525274	x	x	x							
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	MARLBOROUGH	Mt Stokes	<i>I. Breitwieser</i> 2110 & <i>A. Wilton</i>	Mar-98	CHR 526396	x	x		x					x	
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	MARLBOROUGH	Altimarlock	<i>K. Hogan</i> 2	Feb-98	CHR 526401	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	MARLBOROUGH	Mt Fyffe	<i>D. Huson</i>	Mar-96	CHR 526403	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	MARLBOROUGH	No Mans Creek	<i>D. Glenny</i> 6897	Mar-97	CHR 530570	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Culliford Basin	<i>D. Glenny</i> 6296	Jan-96	CHR 509815	x		x		x	x		x		
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Garibaldi	<i>A. Wilton</i> & <i>K. Ford</i> 67/98	Mar-98	CHR 513665	x			x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Mt Mytton	<i>D. Glenny</i> 6823	Feb-97	CHR 530497	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Granity Pass	<i>D. Glenny</i> 7364	Feb-98	CHR 559990	x			x			x			
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Poverty Basin	<i>D. Glenny</i> 7375	Feb-98	CHR 560001	x			x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	NELSON	Balloon Hut	<i>D. Glenny</i> 7436	Mar-98	CHR 560065	x		x	x					x	
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	OTAGO	Shotover Saddle	<i>G. Spearpoint</i>	1998	CHR 526416	x	x	x	x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	OTAGO	Earnslaw Burn	<i>K. Wardle</i>	1997	CHR 526449	x			x						
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	WELLINGTON	Trent River	<i>D. Glenny</i> 6920	Mar-97	CHR 559477									x	
<i>G. corymbifera</i> subsp. <i>corymbifera</i>	WESTLAND	Trent River	<i>D. Glenny</i> 6918	Mar-97	CHR 559475	x						x			
<i>G. corymbifera</i> subsp. <i>gracile</i>	OTAGO	Shotover R., Sixteen Mile Creek	<i>A. P Druce</i> 1502	Mar-90	CHR 472094	x		x							
<i>G. corymbifera</i> subsp. <i>gracilis</i>	CANTERBURY	Fagan Downs	<i>J. Irwin</i>	Feb-78	CHR 323378A									x	
<i>G. corymbifera</i> subsp. <i>gracilis</i>	CANTERBURY	Castle Hill Basin	<i>G. Brownlie</i>	Feb-71	CHR 344896	x								x	

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<i>G. corymbifera subsp. gracilis</i>	CANTERBURY	Tekapo, Glenmore Tarns	<i>P. N. Johnson 1423</i>	Dec-98	CHR 518390	x	x	x	x						
<i>G. corymbifera subsp. gracilis</i>	CANTERBURY	Ohau Range	<i>N. Simpson</i>	Jan-97	CHR 526299		x								
<i>G. corymbifera subsp. gracilis</i>	CANTERBURY	Fagan Downs	<i>D. Glenny 7333</i>	Jan-98	CHR 560136	x	x	x	x	x		x			
<i>G. corymbifera subsp. gracilis</i>	CANTERBURY	Cameron Fan	<i>D. Glenny 7335</i>	Jan-98	CHR 560138	x	x	x	x						
<i>G. corymbifera subsp. gracilis</i>	CANTERBURY	Ohau Range, Sawyers Creek	<i>D. Glenny 7354</i>	Feb-98	CHR 560154	x	x	x	x						
<i>G. corymbifera subsp. gracilis</i>	OTAGO	Skippers Creek	<i>D. Glenny 6401</i>	Feb-96	CHR 509926	x	x	x	x						
<i>G. corymbosa</i>		Colombia, Sierra Nevada del Cocuy	<i>H. Barclay & P. Juajibioy 7417</i>	xxx	MO 2710529	x						x			
<i>G. cunninghamii</i>		Victoria, Mt Buffalo	<i>D. Frood</i>	Feb-98	CHR 447024	x						x			
<i>G. decumbens</i>	NELSON	Kakapo Peak	<i>A. P. Druce</i>	Jan-70	CHR 252186	x			x						
<i>G. decumbens</i>	NELSON	Mt Lodestone	<i>A. P. Druce</i>	Jan-75	CHR 277645	x	x	x							
<i>G. decumbens</i>	NELSON	head of Cobb Valley	<i>A. P. Druce</i>	Feb-77	CHR 310378		x								
<i>G. decumbens</i>	NELSON	Anatoki Range	<i>R. Mason</i>	Feb-46	CHR 34919	x	x	x							
<i>G. decumbens</i>	NELSON	Matiri Plateau	<i>A. P. Druce</i>	Mar-79	CHR 354903	x								x	
<i>G. decumbens</i>	NELSON	Matiri Plateau	<i>A. P. Druce</i>	Mar-79	CHR 355066	x	x	x							
<i>G. decumbens</i>	NELSON	Round Lake	<i>I. Breitwieser 2005 & R. Vogt</i>	Jan-96	CHR 516222	x	x	x					x		
<i>G. decumbens</i>	NELSON	Peel Range	<i>D. Glenny 7437</i>	Mar-98	CHR 560059	x	x	x	x					x	
<i>G. decumbens</i>	NELSON	Boulder Lake	<i>D. Glenny 8103b</i>	Jan-00	CHR 565236	x	x	x	x						
<i>G. decumbens</i>	NELSON	Lake Peel	<i>J. A. Hay</i>	Apr-52	CHR 75654									x	
<i>G. decumbens</i>	NELSON	Lake Sylvester	<i>A. F. Mark</i>	Feb-69	OTA 025054	x	x	x							
<i>G. decumbens</i>	NELSON	Lake Sylvester	<i>A. F. Mark</i>	Feb-69	OTA 025890	x	x	x							
<i>G. dianthoides</i>		Peru, Challuayaco	<i>A. Sagastegui A. 8405</i>	xxx	MO 2922443.	x						x			
<i>G. diemensis ssp. diemensis</i>		Tasmania, Newdegate Pass	<i>A. T. Dobson 77124</i>	Feb-77	CHR 314353	x								x	
<i>G. diemensis subsp. diemensis</i>		Tasmania, Mt St Anne	<i>B. Brown</i>	Apr-96	CHR 526451	x					x				
<i>G. diemensis subsp. plantaginea</i>		Tasmania, Ben Lomond	<i>A. T. Dobson</i>	Mar-77	CHR 398064	x						x			
<i>G. divisa</i>	CANTERBURY	Ashburton Mountains	<i>T. H. Potts</i>	no date	WELT 4714									x	
<i>G. divisa</i>	OTAGO	Fohn Saddle	<i>D. Glenny 8648</i>	Jan-02	CHR 524692									x	

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<i>G. divisa</i>	OTAGO	Shotover Saddle	<i>G. Spearpoint</i>	1998	CHR 526417	x	x	x	x			x			
<i>G. divisa</i>	OTAGO	Earnslaw Burn	<i>K. Wardle</i>	1998	CHR 526419	x	x	x							
<i>G. divisa</i>	OTAGO	Ferguson Creek	<i>K. Wardle</i>	Apr-97	CHR 526440	x			x	x					
<i>G. divisa</i>	OTAGO	Gillespie Pass	<i>B. Brown</i>	Mar-97	CHR 526443	x	x	x						x	
<i>G. divisa</i>	OTAGO	Pisa Range	<i>D. Glenny 7668</i>	Jan-99	CHR 529424		x								
<i>G. divisa</i>	OTAGO	Rock and Pillar Range	<i>D. Glenny 7701</i>	Jan-99	CHR 529454	x	x	x							
<i>G. divisa</i>	OTAGO	Harris Saddle	<i>D. Glenny 6872</i>	Feb-97	CHR 530548	x	x	x							
<i>G. divisa</i>	OTAGO	Harris Saddle	<i>D. Glenny 6874</i>	Feb-97	CHR 559435									x	
<i>G. divisa</i>	OTAGO	Polnoon Burn	<i>D. Glenny 7315</i>	Dec-97	CHR 559587	x	x	x							
<i>G. divisa</i>	OTAGO	Rock and Pillar Range	<i>A. F. Mark</i>	Mar-68	OTA 21733	x								x	
<i>G. divisa</i>	SOUTHLAND	Gertrude Saddle	<i>D. Glenny 6850</i>	Feb-97	CHR 530527	x	x	x					x		
<i>G. divisa</i>	SOUTHLAND	Lake Wapiti	<i>D. Glenny 7458</i>	Apr-98	CHR 560085	x	x	x							
<i>G. divisa</i>	SOUTHLAND	Lake Wapiti	<i>D. Glenny 7476</i>	Apr-98	CHR 560103	x	x	x	x					x	
<i>G. divisa</i>	WESTLAND	Hitchin Range	<i>G. Spearpoint</i>	Dec-98	CHR 518969	x	x	x						x	
<i>G. divisa</i> x <i>G. serotina</i>	OTAGO	Mt Earnslaw, Kea Basin	<i>A. P. Druce 1400</i>	Feb-92	CHR 471992	x								x	
<i>G. divisa</i> x <i>G. serotina</i>	OTAGO	Rock and Pillar Range	<i>J. Talbot</i>	Jan-79	OTA 37795									x	
<i>G. filipes</i>	NELSON	Mt Arthur	<i>T. F. Cheeseman</i>	Jan 1886	AK 7160									x	
<i>G. filipes</i>	NELSON	Garibaldi Range	<i>K. Ford 61/98</i>	Mar-98	CHR 510620	x								x	
<i>G. filipes</i>	NELSON	Mt Mytton	<i>D. Glenny 6816</i>	Feb-97	CHR 530490	x	x	x	x						
<i>G. filipes</i>	NELSON	Mt Owen	<i>D. Glenny 7374</i>	Feb-98	CHR 560002	x	x	x	x			x	x		
<i>G. filipes</i>	NELSON	Garibaldi Range	<i>D. Glenny 7421</i>	Mar-98	CHR 560052	x		x						x	
<i>G. filipes</i>	NELSON	Horseshoe Basin on Mt Arthur	<i>D. Glenny 7441</i>	Mar-98	CHR 560069	x	x	x		x				x	
<i>G. foliosa</i>		Ecuador, Cotopaxi	<i>J. D. Boeke 575</i>	xxx	MO 2697314.	x						x			
<i>G. foliosa</i>		Ecuador	<i>S. Laegaard 53880</i>	xxx	QCA (not seen)	x								x	
<i>G. gibbsii</i>	SOUTHLAND	Mt Anglem	<i>H. D. Wilson</i>	Jan-79	CHR 355442	x								x	
<i>G. gibbsii</i>	SOUTHLAND	Mt Anglem	<i>D. Glenny 6346</i>	Jan-96	CHR 509867	x	x		x						

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<i>G. gibbsii</i>	SOUTHLAND	Mt Anglem	<i>D. Glenny 6355</i>	Jan-96	CHR 509878	x				x		x			
<i>G. gibbsii</i>	SOUTHLAND	Stewart Island	<i>F. G. Gibbs</i>	no date	WELT 4709										
<i>G. gibbsii</i>	SOUTHLAND	Mt Anglem	<i>F. G. Gibbs</i>	Jan-07	WELT 47783									x	
<i>G. grisebachii</i>	CANTERBURY	Rangitata River, Mt Potts	<i>J. B. Armstrong</i>	no date	CHR s.n.									x	
<i>G. grisebachii</i>	CANTERBURY	L. Ellesmere	<i>I. A. Clarke</i>	Feb-66	CHR 150821									x	
<i>G. grisebachii</i>	CANTERBURY	Lake Georgina	<i>J. Clarke</i>	Mar-68	CHR 182525									x	
<i>G. grisebachii</i>	CANTERBURY	Lake Sarah	<i>D. M. Post 357</i>	Dec-69	CHR 201912									x	
<i>G. grisebachii</i>	CANTERBURY	Hunter Hills, Weaner Run	<i>B. H. Macmillan</i>	Apr-73	CHR 238527									x	
<i>G. grisebachii</i>	CANTERBURY	Hooker Valley	<i>H. D. Wilson</i>	Feb-72	CHR 254015									x	
<i>G. grisebachii</i>	CANTERBURY	Fagan Downs	<i>J. B. Irwin</i>	Feb-78	CHR 323377A									x	
<i>G. grisebachii</i>	CANTERBURY	Two Thumbs Range	<i>A. P. Druce</i>	Mar-85	CHR 402135									x	
<i>G. grisebachii</i>	CANTERBURY	Hakataramea	<i>B. Molloy</i>	Feb-96	CHR 510005					x					
<i>G. grisebachii</i>	CANTERBURY	Eric Stream	<i>S. Courtney</i>	Mar-96	CHR 526399		x								
<i>G. grisebachii</i>	CANTERBURY	Kettlehole	<i>D. Glenny 6905</i>	Mar-97	CHR 530578	x		x							
<i>G. grisebachii</i>	CANTERBURY	Lake Sarah	<i>D. Glenny 6905</i>	Mar-97	CHR 530578									x	
<i>G. grisebachii</i>	CANTERBURY	Mt Oxford, Whites Creek	<i>R. Mason 3256</i>	Apr-55	CHR 89326									x	
<i>G. grisebachii</i>	GISBORNE	Raukumara Ra, Kopua-Tarati Ridge	<i>M. Heginbotham</i>	Jan-82	CHR 389509									x	
<i>G. grisebachii</i>	GISBORNE	Mt Raukumara	<i>M. Heginbotham</i>	Feb-81	CHR 389535									x	
<i>G. grisebachii</i>	MARLBOROUGH	Tarndale	<i>P. N. Johnson</i>	Mar-81	CHR 363917									x	
<i>G. grisebachii</i>	NELSON	Lewis Pass	<i>M. J. A. Simpson</i>	Feb-75	CHR 274189									x	
<i>G. grisebachii</i>	NELSON	Matiri Range	<i>A. P. Druce</i>	Mar-79	CHR 355229									x	
<i>G. grisebachii</i>	OTAGO	Cascade River mouth	<i>P. N. Johnson</i>	Mar-77	CHR 283632									x	
<i>G. grisebachii</i>	OTAGO	Mt Beta	<i>P. A. Williams, P. Wardle</i>	Mar-79	CHR 371519	x		x							
<i>G. grisebachii</i>	OTAGO	Forgotten River	<i>B. Brown</i>	Jan-96	CHR 510004	x	x				x				
<i>G. grisebachii</i>	OTAGO	Siberia Stream	<i>B. Brown</i>	Mar-97	CHR 526442		x							x	
<i>G. grisebachii</i>	OTAGO	Lake Harris	<i>D. Glenny 6876</i>	Apr-96	CHR 530552	x		x							

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<i>G. grisebachii</i>	OTAGO	Rees Valley	<i>D. Glenny 6884</i>	Mar-97	CHR 559445	x	x	x	x						
<i>G. grisebachii</i>	OTAGO	Lake Harris	<i>D. Petrie</i>	Feb-11	WELT 4710									x	
<i>G. grisebachii</i>	SOUTHLAND	Awarua Bay	<i>R. Powell</i>	no date	CHR 358000									x	
<i>G. grisebachii</i>	SOUTHLAND	Garvie Mountains	<i>D. Glenny 6380</i>	Feb-96	CHR 509906		x								
<i>G. grisebachii</i>	SOUTHLAND	Garvie Mountains	<i>D. Glenny 6385</i>	Feb-96	CHR 509911		x			x				x	
<i>G. grisebachii</i>	SOUTHLAND	Mavora Hills	<i>P. N. Johnson 1360</i>	Feb-97	CHR 511788	x		x							
<i>G. grisebachii</i>	SOUTHLAND	Lake Manapouri	<i>P. N. Johnson 1377</i>	Mar-97	CHR 512377		x							x	
<i>G. grisebachii</i>	SOUTHLAND	Manapouri	<i>P. N. Johnson 1377</i>	Mar-97	CHR 512377	x		x							
<i>G. grisebachii</i>	SOUTHLAND	Livingstone Mountains	<i>P. N. Johnson 1407</i>	Jan-98	CHR 515002	x	x	x	x			x			
<i>G. grisebachii</i>	SOUTHLAND	Lake Marion	<i>D. Glenny 6838</i>	Feb-97	CHR 530513		x							x	
<i>G. grisebachii</i>	SOUTHLAND	Gertrude Valley	<i>D. Glenny 6843</i>	Feb-97	CHR 530520	x	x	x							
<i>G. grisebachii</i>	TARANAKI	Pouakai Range	<i>A. P. Druce</i>	Feb-58	CHR 86969									x	
<i>G. grisebachii</i>	WELLINGTON	Rimutaka Range	<i>A. P. Druce</i>	Jan-47	CHR 116403									x	
<i>G. grisebachii</i>	WELLINGTON	Whana Huia Range	<i>A. P. Druce</i>	Feb-46	CHR 116409									x	
<i>G. grisebachii</i>	WELLINGTON	Ruahine Ra, SW of Takapai	<i>A. P. Druce</i>	Mar-70	CHR 209451									x	
<i>G. grisebachii</i>	WELLINGTON	SW of L. Taupo, Mt Tihia	<i>A. P. Druce</i>	Apr-74	CHR 273210									x	
<i>G. grisebachii</i>	WELLINGTON	Rangitikei River	<i>A. P. Druce</i>	Feb-75	CHR 277362									x	
<i>G. grisebachii</i>	WELLINGTON	Oroua River	<i>A. P. Druce</i>	Apr-78	CHR 323640									x	
<i>G. grisebachii</i>	WELLINGTON	Rangitikei R., Ohutu Stream	<i>C. C. Ogle 1568</i>	Feb-88	CHR 440135									x	
<i>G. grisebachii</i>	WELLINGTON	Tararua Ra, Mt Kariparoro	<i>A. P. Druce</i>	Feb-89	CHR 472118									x	
<i>G. grisebachii</i>	WELLINGTON	Mt Wainui	<i>M. C. Roberts</i>	Apr-98	CHR 51855									x	
<i>G. grisebachii</i>	WELLINGTON	Rimutaka Saddle	<i>D. Glenny 6780</i>	Jan-97	CHR 530463	x		x							
<i>G. grisebachii</i>	WELLINGTON	Tararua Ra, Te Matawai Hut	<i>R. Mason</i>	Mar-47	CHR 58163									x	
<i>G. grisebachii</i>	WELLINGTON	Tararua Ra, Mt Waiopahu between Rotoaira and the base of	<i>R. Mason</i>	Apr-48	CHR 62201									x	
<i>G. grisebachii</i>	WELLINGTON	Tongariro	<i>J. C. Bidwill</i>	no date	K (photograph seen).		x								
<i>G. grisebachii</i>	WELLINGTON	Rimutaka Saddle	<i>D. Glenny 6805</i>	Jan-97	CHR		x								

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<i>G. grisebachii</i>	WESTLAND	Tuhua	<i>W. Mackay</i>	Feb-27	CHR 60221	x		x							
<i>G. grisebachii</i>	WESTLAND	Franz Josef	<i>M. Simpson 905</i>	Jan-54	CHR 77741	x							x		
<i>G. grisebachii</i>		Southern Alps	<i>J. B. Armstrong</i>	no date	AK 7179									x	
<i>G. grisebachii</i> (" <i>G. matthewsii</i> ")	OTAGO	Harris Saddle	<i>D. Glenny 6876</i>	Feb-97	CHR 530552	x	x								
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Flagstaff	<i>G. Simpson</i>	Feb-48	CHR 109503									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Maungatua	<i>D. M. Post 373</i>	Sep-70	CHR 201928									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Old Man Range, Campbell Ck	<i>A. P. Druce</i>	Mar-87	CHR 395305									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Lammerlaw Range, Teviot Swamp	<i>P. N. Johnson</i>	Jan-85	CHR 417908									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Hunter Valley	<i>P. Wardle</i>	Mar-88	CHR 464543									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Nevis Valley	<i>A. P. Druce</i>	Feb-92	CHR 472059									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	OTAGO	Swampy Hill	<i>H. H. Allan</i>	Jan-48	CHR 76517									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Lake Monk	<i>M. J. A. Simpson 1984</i>	Jan-60	CHR 115996									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Rakeahua River	<i>R. Melville</i>	Feb-62	CHR 144620									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Mt Rakeahua Hut	<i>L. J. Dumbleton</i>	Feb-68	CHR 182495									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Wet Jacket Arm	<i>D. R. Given 72180</i>	Feb-72	CHR 227452									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Colac Bay	<i>R. Mason, E. M. Chapman</i>	Feb-73	CHR 238142									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Riverton-Invercargill	<i>R. Powell</i>	Mar-74	CHR 259703									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Tutuko Valley	<i>P. N. Johnson</i>	Jan-77	CHR 283523									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Taiaroa Bush	<i>P. N. Johnson</i>	Mar-82	CHR 353854									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Stewart Is, Ringaringa River	<i>H. D. Wilson</i>	Mar-80	CHR 368811									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Oreti R. near S.Mavora River	<i>A. P. Druce</i>	Mar-89	CHR 394549									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Waitutu	<i>C. C. Ogle 1104</i>	Jan-84	CHR 417133									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Weydon Burn	<i>A. J. D. Barker</i>	Jan-38	CHR 516008									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Dusky Sound, Supper Cove	<i>H. H. Allan</i>	Feb-46	CHR 55387									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Oreti Beach	<i>R. Mason</i>	Feb-52	CHR 75890									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Clinton-Mataura Rd	<i>R. Mason</i>	Feb-52	CHR 75940									x	

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<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Wilmot Pass	<i>G. Simpson</i>	Jan-48	CHR 76518									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Wilmot Flat Hut	<i>G. Simpson</i>	Jan-48	CHR 76523									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Dome Burn	<i>A. P. Druce</i>	Mar-77	CHR 395339									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	SOUTHLAND	Otaimai	<i>A. J. Healy</i>	Apr-45	CHR 51335									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	WESTLAND	Marks Flat	<i>P. Wardle</i>	Feb-72	CHR 223931									x	
<i>G. grisebachii</i> (as <i>G. matthewsii</i>)	WESTLAND	Lake Sweeney	<i>P. Wardle, D. A. Campbell</i>	Feb-78	CHR 280755									x	
<i>G. grisebachii</i> and <i>G. montana</i> subsp. <i>ionostigma</i> , mixed	WELLINGTON	Whana Huia Range	<i>A. P. Druce</i>	Feb-67	CHR 165851-4	x								x	
<i>G. grisebachii</i> x <i>G. montana</i> subsp. <i>ionostigma</i>	WELLINGTON	Tararua Range, near Anderson's Hut	<i>A. P. Druce</i>	Mar-69	CHR 190614	x								x	
<i>G. grisebachii</i>	CANTERBURY	Okuku saddle	<i>Y. H. Elder</i>	Apr-69	CHR 191777									x	
<i>G. impressinervia</i>	CANTERBURY	Lewis Pass, Mt Technical	<i>M. Newfield 1/98 & D. Banks</i>	Feb-98	CHR 526413	x	x	x						x	
<i>G. impressinervia</i>	NELSON	Glasgow Range	<i>A. P. Druce</i>	Feb-86	CHR 394530	x							x		
<i>G. impressinervia</i>	NELSON	Mt Mantell	<i>G. Jane</i>	Mar-98	CHR 516245	x	x	x	x						
<i>G. impressinervia</i>	NELSON	Lyell Range	<i>D. Glenney 8408</i>	Mar-01	CHR 526311	x		x							
<i>G. impressinervia</i>	NELSON	Mt Fleming	<i>G. Jane</i>	Apr-98	CHR 526404	x		x							
<i>G. impressinervia</i>	NELSON	Buckland Peaks	<i>K. Ford B/5</i>	Mar-96	CHR 526448	x	x	x	x	x					
<i>G. impressinervia</i>	NELSON	Mt Euclid	<i>D. Glenney 8119</i>	Feb-00	CHR 527450	x		x							
<i>G. impressinervia</i>	NELSON	Mt Euclid	<i>D. Glenney 8143</i>	Feb-00	CHR 527481	x		x							
<i>G. impressinervia</i>	WELLINGTON	Trent Saddle	<i>D. Glenney 6908</i>	Mar-97	CHR 559466	x	x	x							
<i>G. lilliputiana</i>	OTAGO	Dunstan Mountains	<i>A. Mark & R. Allen</i>	Feb-85	CHR 417292	x	x		x						
<i>G. lilliputiana</i>	OTAGO	Lauder Creek	<i>D. Bruce</i>	1985	CHR 418480	x	x						x		
<i>G. lilliputiana</i>	OTAGO	Lauder Creek	<i>D. Bruce</i>	Jan-85	CHR 460522										
<i>G. lilliputiana</i>	OTAGO	Dunstan Mountains	<i>D. Bruce</i>	Jan-85	CHR 461347		x								
<i>G. lilliputiana</i>	OTAGO	St Bathans Range	<i>N. Simpson</i>	Jan-02	CHR 542369	x					x				
<i>G. lilliputiana</i>	OTAGO	Dunstan Mountains	<i>A. F. Mark</i>	Feb-85	OTA 41684		x						x		
<i>G. lineata</i>	SOUTHLAND	Longwood Range	<i>T. Kirk</i>	Jan 1887	AK 7161 & 7163									x	
<i>G. lineata</i>	SOUTHLAND	Stewart Is, Granite Knob	<i>C. J. Webb 78/17</i>	Dec-78	CHR 327342		x								

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<i>G. lineata</i>	SOUTHLAND	Ajax Bog	<i>P. N. Johnson</i>	Nov-75	CHR 364169	x	x						x		
<i>G. lineata</i>	SOUTHLAND	Mt Anglem	<i>D. Glenny 6345</i>	Jan-96	CHR 509866	x					x				
<i>G. lineata</i>	SOUTHLAND	Mt Anglem	<i>D. Glenny 6356</i>	Jan-96	CHR 509879		x								
<i>G. lineata</i>	SOUTHLAND	Lake Wapiti	<i>D. Glenny 7475</i>	Apr-98	CHR 560102	x	x		x	x					
<i>G. lineata</i>	SOUTHLAND	Lake Manapouri, Mt Wilmott	<i>G. Simpson</i>	Jan-48	CHR 75699									x	
<i>G. lineata</i>	SOUTHLAND	Mt Wilmott	<i>G. Simpson</i>	no date	CHR 76316		x								
<i>G. lineata</i>	SOUTHLAND	Longwood Range	<i>T. Kirk</i>	Jan 1887	WELT 4708									x	
<i>G. luteoalba</i>	NELSON	Lookout Range	<i>C. J. Webb 76137</i>	Apr-76	CHR 283742		x								
<i>G. luteoalba</i>	NELSON	Hope Range	<i>G. Jane</i>	Mar-98	CHR 516247	x	x	x	x						
<i>G. luteoalba</i>	NELSON	Lookout Range	<i>D. Glenny 7361</i>	Feb-98	CHR 559987	x	x	x	x	x		x	x		
<i>G. magellanica</i>		Falkland Islands	<i>D. M. Moore 790</i>	Feb-64	CHR 183097									x	
<i>G. magellanica</i>		Argentina, Rio Negro, Cerro Catedral	<i>P. Wardle & S. Wagstaff 97083</i>	Jan-97	CHR 514046	x					x				
<i>G. magellanica</i>		Chile	<i>E. J. Godley 931</i>	Jan-59	CHR 534629	x			x						
<i>G. magnifica</i>	CANTERBURY	Miromiro	<i>D. Petrie</i>	Nov-17	CANU 2931	x	x	x							
<i>G. magnifica</i>	CANTERBURY	Mount Captain	<i>T. Kirk</i>	no date	WELT 4715	x	x	x							
<i>G. magnifica</i>	MARLBOROUGH	Barefell	<i>J. McLintock</i>	Feb-00	CHR 526300	x	x		x						
<i>G. magnifica</i>	MARLBOROUGH	Barefell	<i>D. Glenny 7451</i>	Mar-98	CHR 529216	x	x	x	x	x				x	
<i>G. magnifica</i>	MARLBOROUGH	Mt Barefell	<i>D. Glenny 6900</i>	Mar-97	CHR 530573	x	x	x							
<i>G. montana ssp. montana</i>	SOUTHLAND	Dusky Sound	<i>G. Forster</i>	no date	BM (photograph seen)								x	x	
<i>G. montana ssp. montana</i>	SOUTHLAND	Homer Tunnel east portal	<i>D. Glenny 6840</i>	Feb-97	CHR 559402									x	
<i>G. montana ssp. montana</i>	SOUTHLAND	Homer Tunnel west portal	<i>D. Glenny 6842</i>	Feb-97	CHR 559406									x	
<i>G. montana subsp. ionostigma</i>	GISBORNE	Mt Hikurangi	<i>I. Breitwieser 2062</i>	Jan-98	CHR 526397	x	x	x	x	x		x	x		
<i>G. montana subsp. ionostigma</i>	WELLINGTON	Mt Holdsworth	<i>M. J. Bayly 571, 572, 573</i>	Feb-97	CHR 526394	x	x	x							
<i>G. montana subsp. ionostigma</i>	WELLINGTON	Whana Huia Range	<i>D. Glenny 6799</i>	Jan-97	CHR 530479	x			x						
<i>G. montana subsp. ionostigma</i>	WELLINGTON	Whana Huia Range	<i>D. Glenny 6794</i>	Jan-97	CHR 559362	x	x	x							
<i>G. montana subsp. ionostigma</i>	WELLINGTON	Whana Huia Range	<i>D. Glenny 6795</i>	Jan-97	CHR 559363	x	x	x							

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<i>G. montana subsp. ionostigma</i>	WELLINGTON	Whana Huia Range	<i>D. Glenny 6798</i>	Jan-97	CHR 559365		x								
<i>G. montana subsp. ionostigma</i>	WELLINGTON	Whana Huia Range	<i>D. Glenny 6799</i>	Jan-97	CHR 559366	x	x	x							
<i>G. montana subsp. montana</i>	CANTERBURY	Arthur's Pass	<i>T. Kirk</i>	no date	WELT 4717									x	
<i>G. montana subsp. montana</i>	CANTERBURY	Island Pass	<i>D. Glenny 7452</i>	Mar-98	CHR 560079	x		x							
<i>G. montana subsp. montana</i>	NELSON	Mt Mytton	<i>D. Glenny 6818</i>	Feb-97	CHR 559379	x	x	x							
<i>G. montana subsp. montana</i>	NELSON	Mt Arthur	<i>D. Glenny 6836</i>	Feb-97	CHR 559397	x	x	x	x	x					
<i>G. montana subsp. montana</i>	NELSON	Lookout Range	<i>D. Glenny 7357</i>	Feb-98	CHR 559983	x		x	x			x			
<i>G. montana subsp. montana</i>	NELSON	Loveridge Peak	<i>D. Glenny 7446</i>	Mar-98	CHR 559983	x			x						
<i>G. montana subsp. montana</i>	NELSON	St Arnaud Range	<i>D. Glenny 7426</i>	Mar-98	CHR 560057	x		x							
<i>G. montana subsp. montana</i>	NELSON	Balloon Hut	<i>D. Glenny 7349</i>	Feb-98	CHR 560067		x								
<i>G. montana subsp. montana</i>	NELSON	Mt Arthur	<i>B. V. Sneddon</i>	xxx	WELTU 15673 (not seen)									x	
<i>G. montana subsp. montana</i>	OTAGO	Lake Harris	<i>D. Glenny 6870</i>	Feb-97	CHR 559431	x	x	x	x				x		
<i>G. montana subsp. montana</i>	OTAGO	Harris Saddle	<i>D. Glenny 6873</i>	Feb-97	CHR 559434	x	x	x							
<i>G. montana subsp. montana</i>	OTAGO	Kea Basin	<i>D. Glenny 6882</i>	Mar-97	CHR 559443	x	x		x						
<i>G. montana subsp. montana</i>	OTAGO	Lake Harris	<i>D. Petrie</i>	Feb-11	WELT 2723									x	
<i>G. montana subsp. montana</i>	SOUTHLAND	Wet Jacket Arm	<i>D. Given 72389</i>	Feb-72	CHR 230614		x								
<i>G. montana subsp. montana</i>	SOUTHLAND	Longwood Range	<i>P. N. Johnson 1534</i>	Feb-97	CHR 511782	x			x						
<i>G. montana subsp. montana</i>	SOUTHLAND	Borland Saddle	<i>P. N. Johnson 1358</i>	Feb-97	CHR 511786	x	x	x	x						
<i>G. montana subsp. montana</i>	SOUTHLAND	West Homer Tunnel	<i>D. Glenny 6840</i>	Feb-97	CHR 559402	x	x								
<i>G. montana subsp. montana</i>	SOUTHLAND	East Homer Tunnel	<i>D. Glenny 6842</i>	Feb-97	CHR 559406	x	x								
<i>G. montana subsp. montana</i>	SOUTHLAND	Lake Wapiti	<i>D. Glenny 7466</i>	Apr-98	CHR 560091		x								
<i>G. montana subsp. montana</i>	SOUTHLAND	Princess Range	<i>J. Speden</i>	Jan-24	WELT 4720									x	
<i>G. montana subsp. montana</i>	WESTLAND	Omoeroa/Waikukupa plateau	<i>P. Wardle</i>	Jul-70	CHR 203677A	x								x	
<i>G. montana subsp. montana</i>	WESTLAND	Kelly Saddle	<i>D. Glenny 6464</i>	Mar-96	CHR 509989	x		x			x			x	
<i>G. montana subsp. montana</i>	WESTLAND	Haast, Headlong Spur	<i>G. Spearpoint</i>	Apr-98	CHR 518957		x								
<i>G. montana subsp. montana</i>	WESTLAND	McArthur Range	<i>P. Knightbridge</i>	Apr-01	CHR 526438	x		x						x	

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<i>G. montana subsp. montana</i>	WESTLAND	Harman	<i>D. Glenney 6932</i>	Apr-97	CHR 530601	x		x							
<i>G. montana subsp. montana</i>	WESTLAND	Lake Gault	<i>D. Glenney 6891</i>	Mar-97	CHR 559452	x		x		x				x	
<i>G. montana subsp. montana</i>	WESTLAND	Lake Sweeney	<i>D. Glenney 7385</i>	Feb-98	CHR 560015	x		x							
<i>G. montana subsp. montana</i>	WESTLAND	Mt Fox	<i>D. Glenney 7402</i>	Feb-98	CHR 560033	x		x							
<i>G. montana subsp. montana</i>	WESTLAND	Mt Mason	<i>D. Glenney 6912</i>	Mar-97	CHR 530584	x		x							
<i>G. montana var. stolonifera</i>	NELSON	Mount Rochfort	<i>W. Townson</i>	no date	AK 200251										x
<i>G. montana var. stolonifera</i>	NELSON	Mount Rochfort	<i>W. Townson</i>	no date	AK 7213										x
<i>G. montana var. stolonifera</i>	NELSON	Glasgow Range	<i>G. Loh</i>	Dec-78	CHR 359085	x		x							
<i>G. montana var. stolonifera</i>	NELSON	Mt Rochfort	<i>M. J. A.. Simpson 7840</i>	Apr-76	CHR 439804	x		x							
<i>G. montana var. stolonifera</i>	NELSON	Sewell Peak	<i>D. Glenney 6418</i>	Mar-96	CHR 509944	x	x	x	x	x	x				
<i>G. montana var. stolonifera</i>	NELSON	Buckland Peaks	<i>D. Glenney 6448</i>	Mar-96	CHR 509975		x								
<i>G. montana var. stolonifera</i>	NELSON	Buckland Peaks	<i>D. Glenney 6458</i>	Mar-96	CHR 509983	x	x	x							
<i>G. montana var. stolonifera</i>	NELSON	Mt Mantell	<i>G. Jane</i>	Mar-98	CHR 516244		x								
<i>G. montana var. stolonifera</i>	NELSON	Mt Rochfort	<i>D. Glenney 6945</i>	May-97	CHR 526295	x	x	x							
<i>G. montana var. stolonifera</i>	NELSON	Lyell	<i>D. Glenney 8406</i>	Mar-01	CHR 526310	x		x							
<i>G. montana var. stolonifera</i>	NELSON	Te Kuha	<i>D. Glenney 8412</i>	Mar-01	CHR 526315	x		x							
<i>G. montana var. stolonifera</i>	NELSON	Mt Fleming	<i>G. Jane</i>	Apr-98	CHR 526404	x	x	x							
<i>G. montana var. stolonifera</i>	NELSON	Buckland Peaks	<i>P. Lockhart</i>	Mar-99	CHR 526411	x	x	x							
<i>G. montana var. stolonifera</i>	NELSON	Lookout Range	<i>D. Glenney 7357</i>	Feb-98	CHR 559983	x							x		
<i>G. montana var. stolonifera</i>	WESTLAND	Croesus Knob	<i>P. Suisted</i>	Apr-98	CHR 516249	x			x				x		
<i>G. muelleriana subsp. alpestris</i>		Australia, Mt Kosciusko	<i>J. Ward 96048</i>	Jan-96	CHR 526435	x					x				
<i>G. myriantha</i>		Bolivia	<i>S. Halloy 4271</i>	xxx	C&F germplasm accession 1404	x					x				
<i>G. narcissoides</i>		Bolivia	<i>S. Halloy 4268</i> <i>H.G. Barclay & P. Juajibioy</i>	xxx	C&F germplasm accession 1399	x					x				
<i>G. nummularifolia</i>		Cordillera Oriental	<i>8837</i>	xxx	MO 2710534	x							x		
<i>G. ottonis</i>		Chile, Ortega-Arrayan	<i>O. Zollner</i>	xxx	MO 2981384	x							x		

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<i>G. patula</i>	CANTERBURY	Clarence Valley	<i>D. Glenny 6282</i>	Jan-96	CHR 509800		x								
<i>G. patula</i>	CANTERBURY	Lake Tennyson	<i>D. Glenny 6282</i>	Jan-96	CHR 509800	x		x							
<i>G. patula</i>	MARLBOROUGH	Raglan Range	<i>A. P. Druce</i>	Feb-80	CHR 365714	x			x						
<i>G. patula</i>	MARLBOROUGH	Upper Wairau, Hare Creek	<i>A. P. Druce</i>	Mar-87	CHR 401232	x	x								
<i>G. patula</i>	NELSON	Cobb Valley	<i>F. G. Gibbs 369</i>	no date	CHR 118637	x								x	
<i>G. patula</i>	NELSON	Travers Range	<i>M. J. A. Simpson 3084</i>	Mar-61	CHR 120774	x	x	x							
<i>G. patula</i>	NELSON	Mt Robert	<i>M. J. A. Simpson 6871</i>	Feb-72	CHR 227750		x								
<i>G. patula</i>	NELSON	Gordons Knob	<i>A. P. Druce</i>	Feb-80	CHR 365715	x			x						
<i>G. patula</i>	NELSON	Cobb Valley	<i>D. Glenny 6777</i>	Jan-97	CHR 530458		x								
<i>G. patula</i>	NELSON	Cobb Valley	<i>D. Glenny 6772</i>	Jan-97	CHR 530458 ex glasshouse	x		x				x			
<i>G. patula</i>	NELSON	Cobb Valley, Mytton Creek	<i>D. Glenny 6824b</i>	Feb-97	CHR 541820	x	x	x		x					
<i>G. patula</i>	NELSON	Fenella Hut	<i>D. Glenny 6750</i>	Jan-97	CHR 559321	x	x	x					x		
<i>G. patula</i>	NELSON	St Arnaud Range	<i>D. Glenny 7428</i>	Mar-98	CHR 560059	x			x						
<i>G. patula</i>	NELSON	Mt Travers	<i>A. P. Druce</i>	Apr-47	CHR 79599	x			x						
<i>G. patula</i>	NELSON	Rotoiti	<i>T. Kirk</i>	Jan 1875	WELT 47583									x	
<i>G. patula</i>	WESTLAND	Mt Mason	<i>D. Glenny 6899</i>	Mar-97	CHR					x					
<i>G. pleurogynoides</i>		Tasmania, L. Adelaide	<i>B. Brown</i>	Apr-96	CHR 526452	x					x				
<i>G. polysperes</i>		Tasmania	<i>B. Brown</i>	Apr-96	CHR 526450	x					x				
<i>G. saxosa</i>	SOUTHLAND	Dusky Sound	<i>G. Forster</i>	xxx	K photograph seen										
<i>G. saxosa</i>	SOUTHLAND	Stewart Island	<i>Rev. Mr Stack</i>	no date	CHR s.n.									x	
<i>G. saxosa</i>	SOUTHLAND	Big South Cape	<i>B. Bell</i>	Apr-61	CHR 115337	x			x						
<i>G. saxosa</i>	SOUTHLAND	Codfish Is.	<i>I. M. Ritchie</i>	Dec-66	CHR 180204	x			x						
<i>G. saxosa</i>	SOUTHLAND	West Cape	<i>P. K. Dorizac</i>	Dec-67	CHR 183408	x			x						
<i>G. saxosa</i>	SOUTHLAND	Oreti	<i>S. G. Royds</i>	Apr-69	CHR 191761	x			x						
<i>G. saxosa</i>	SOUTHLAND	Bluff	<i>S. G. Royds</i>	Apr-69	CHR 191762	x			x						
<i>G. saxosa</i>	SOUTHLAND	Bluff	<i>D. M. Post</i>	Oct-70	CHR 201930	x			x						

TAXON	LAND DISTRICT	LOCALITY	COLLECTOR	DATE	ACCESSION	P	A	B	C	D	E	F	G	H	I
<i>G. saxosa</i>	SOUTHLAND	Breaksea	<i>P. N. Johnson</i>	Dec-74	CHR 261516	x			x						
<i>G. saxosa</i>	SOUTHLAND	Curio Bay	<i>C. J. Webb</i>	Mar-78	CHR 283978	x			x						
<i>G. saxosa</i>	SOUTHLAND	Muttonbird Is., Betsy I.	<i>I. M. Ritchie</i>	Jul-67	CHR 401445	x	x		x						
<i>G. saxosa</i>	SOUTHLAND	False Inlet	<i>P. N. Johnson</i>	Jan-94	CHR 494684	x			x						
<i>G. saxosa</i>	SOUTHLAND	Big Bungaree Beach	<i>D. Glenny 6372</i>	Feb-96	CHR 509898	x	x		x		x	x			
<i>G. saxosa</i>	SOUTHLAND	Waipapa Point	<i>B. Rance 2/98</i>	Feb-98	CHR 526415	x	x			x		x			
<i>G. saxosa</i>	SOUTHLAND	Stewart Is, Mason Bay	<i>J. F. Findlay</i>	Jan-52	CHR 78044	x			x						
<i>G. saxosa</i>	SOUTHLAND	Dog Island	<i>T. Kirk</i>	Jan 1884	WELT 47548										x
<i>G. saxosa</i>	SOUTHLAND	Waipapa Pt	<i>W. D. Burke</i>	xxx	WELTU 1466		x							x	
<i>G. scopulorum</i>	NELSON	Rocks near the sea at Charlestown	<i>W. Townson 504</i>	no date	AK 7316										x
<i>G. scopulorum</i>	NELSON	Charleston	<i>Anon. P. J. de Lange 1471 & D. Norton</i>	no date	CHR 10972	x								x	
<i>G. scopulorum</i>	NELSON	Charleston		Aug-92	CHR 479209		x								
<i>G. scopulorum</i>	NELSON	Charleston	<i>D. Glenny 6326</i>	Jan-96	CHR 509848	x	x		x						
<i>G. serotina</i>	CANTERBURY	Upper Canterbury Plains upper Canterbury Plain near Springfield	<i>L. Cockayne</i>	Apr 1899	AK 209538										x
<i>G. serotina</i>	CANTERBURY	Springfield	<i>L. Cockayne</i>	Apr 1899	AK 7240										x
<i>G. serotina</i>	CANTERBURY	Lees Valley	<i>L. R. Stemmer</i>	Mar-74	CHR 259206	x	x	x							
<i>G. serotina</i>	CANTERBURY	Lake Lyndon	<i>C. J. Webb</i>	Mar-76	CHR 283763	x								x	
<i>G. serotina</i>	CANTERBURY	Lake Lyndon	<i>D. Glenny 6429</i>	Mar-96	CHR 509956	x	x	x	x						
<i>G. serotina</i>	CANTERBURY	Lake Lyndon	<i>D. Glenny 6906</i>	Mar-97	CHR 530579	x	x	x							
<i>G. serotina</i>	CANTERBURY	Springfield	<i>L. Cockayne</i>	Apr 1899	WELT 4724										x
<i>G. serotina</i>	OTAGO	Maungatua	<i>G. Simpson</i>	Dec-31	CHR 109508	x	x	x							
<i>G. serotina</i>	OTAGO	Lammermoor Range	<i>C. Jensen</i>	Mar-97	CHR 526408	x	x	x							
<i>G. serotina</i>	OTAGO	Sutton	<i>H. Aitchison</i>	Apr-53	OTA 2643	x				x					
<i>G. serotina</i>	OTAGO	Rock and Pillar Ra.	<i>M. Sinclair</i>	Apr-85	OTA 44772	x				x					
<i>G. serotina</i>	OTAGO	Rock and Pillar Range	<i>N. Simpson</i>	Mar-93	CHR 472159	x	x	x	x						
<i>G. serotina</i>	OTAGO	Rock and Pillar Range	<i>N. Simpson</i>	Mar-97	CHR	x			x						

TAXON	LAND DISTRICT	LOCALITY	COLLECTOR	DATE	ACCESSION	P	A	B	C	D	E	F	G	H	I
<i>G. vernicosa</i>	NELSON	Garibaldi Ridge	<i>D. Glenny 7412</i>	Mar-98	CHR 560043	x	x	x							
<i>G. vernicosa</i>	NELSON	Cundy Creek	<i>D. Glenny 7432</i>	Mar-98	CHR 560061	x	x		x						
<i>G. vernicosa</i>	NELSON	Loveridge Peak	<i>D. Glenny 7445</i>	Mar-98	CHR 560073	x		x	x						
<i>G. weberbaueri</i>		Peru, Huascaran N.P.	<i>D. N. Smith et al. 9630</i>	xxx	MO 3307963	x						x			